Manning Diversified Forest Products
Research Trust Fund
MDFP 1/98

MIXLIGHT™ A Flexible Light Transmission Model for Mixed Species Forest Stands

1998– Final Report

September 1998

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Pub # T/429 ISBN# 0-7785-0401-8

Crown characteristics of boreal conifers and application of the light model MIXLIGHT

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The study on which this report is based was partially funded by the Manning Diversified Research Trust Fund (MDRTF). The views, statements and conclusions expressed and the recommendations made in this report are entirely those of the authors and should not be construed as the statements or conclusions of or as expressing the opinions of the MDRFT Committee.

Abstract

Crown characteristics of boreal conifers and application of the light model MIXLIGHT

Regression equations we developed to predict crown dimensions of common boreal forest species needed to calibrate the MIXLIGHT model. Height to live crown was measured on 629 trees from 23 boreal forest sites. Regressions to estimate height to live crown based upon tree and stand variables had an R^2 of 0.74. Besides tree height and diameter, spruce and fir basal area were useful predictors of height to live crown. Crown width was estimated from a 12630 trees in the Peace River Valley. The most important estimators for crown width were height, diameter and stem density. Using the above regression equations as input into the MIXLIGHT model, we estimated the light regime for 39 permanent sample plots of maturing boreal mixedwood stands with understory spruce. Light and other stand variables were then used to predict the growth of understory spruce of a range of height classes. Conifer basal area and grass and lichen cover were the best predictors of spruce growth in the understory.

Acknowledgments

The authors thank Simon Landhausser and Bradley Pinno for assistance, and Tim Vinge for the data set on crown diameters. Funding for this work was provided by grants from Manning Diversified Research Trust Fund and Alberta-Pacific Forest Industries Ltd.

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Introduction

Light regime in the understory is critical for the height growth of spruce seedlings, the abundance of and leaf area of the understory plants and the branching patterns and bole taper of trees. Foresters are interested in manipulating light levels so that they can influence all of the above factors (Smith et al. 1997). In a silvicultural manipulaton of canopy there should be sufficient light to allow the understory trees to grow at an acceptable rate but not so much light that competing vegetation is promoted. These types of prescriptions call for exacting knowledge of the light regime in a stand after partial-logging. Similarly, we need to know the level of light in the lower crown to predict the death and self-pruning of branches of trees (Maquire 1994). Most partial cut silvicultural systems use either basal area/Ha or volume/Ha as a means of prescribing the stocking levels of a stand. The relationship between transmitted light and basal area of a stand after a partial-cut, however, will be confounded by the type of overstory species (e.g. aspen crowns transmit far more light than spruce crowns of trees of the same DBH (Lieffers and Stadt 1994)) and stand condition prior to partial-cutting (dense stands have short crowns compared to the long crown of open-grown trees (Constabel 1995)). In addition the light level at specific spots within the understory is also important in the development of underplanting programs such as envisioned in Lieffers et al. (1996).

The characterization of light in forests has been a key focus of work on forest community dynamics and regeneration (Constabel and Lieffers 1996). Numerous studies have established the dependence of tree and understory growth on available light in stands

(Messier, Honer & Kimmins 1989; Lieffers & Stadt 1994) and microsites (Poulson & Platt 1989; Alaback & Tappeiner 1991; Klinka et al. 1992; McLure & Lee 1993; Poage & Peart 1993; Runkle, Stewart & Veblen 1995). However, adequate measurement of light is time-consuming due to the heterogeneity in space and composition of the canopy, diurnal and seasonal changes in solar position and cloudiness, and leaf-on and off cycles. A number of authors have shown that it is possible to use the well-described laws of solar geometry and information about the canopy structure to predict light regimes in forests at the stand (Norman & Jarvis 1975) and the microsite level (Grace, Jarvis & Norman 1987; Wang & Jarvis 1990; Pukkala, Kuuluvainen & Stenberg 1993; Canham et al. 1994; Cescatti 1997; Ter-Mikaelian et al. 1997).

Forest tenures often cover large areas of mixed composition and have varying amounts of inventory data available for management decisions. There is also a considerable range of stand-tending and harvesting options, from unmanaged to intensive thinning and partial-cut silvicultural systems, all of which have implications for the light regime and vegetation response. Clearly, there is a need for an easily-calibrated, multi-species model of light availability that is flexible enough to produce accurate understory light predictions on a scale appropriate to the inventory data and management goals. Such a model would be of considerable help in studying, planning and managing regeneration in working and research forests (Lieffers et al. 1999).

MIXLIGHT is a simple model that tracks light from both the solar disc and the from 480 different sections of the sky dome and determines the light transmitted between or

through the crowns of the trees in a stand (Stadt and Lieffers 1998). It allows light penetration theory to be applied to existing forest inventory data with minimal calibration and makes light availability predictions for a wide range of forest stands. MIXLIGHT can be run to model the light on a microsite basis or on an average stand basis. MIXLIGHT can generate light predictions from either a complete tree list (an inventory of every tree in the plot) or a minimal list of tree species densities and bole diameter distribution. A complete list includes species, diameter, height, height to the base of the live crown, crown radius, and tree location coordinates. With some forest inventories the full range of data is collected. Often, however, tree height, height to live crown and crown width are not completely measured in inventory plots. What is needed is a good method of estimating these variables (using regression techniques) from other stand and tree characteristics measured in the plots. A objective of this paper is to develop functions that will allow prediction of crown length and diameter and area from stand characteristics. Better estimates of these are needed to make full use of inventory data (PSPs) as input into the light model.

While the importance of estimation of light for the prediction of understory spruce growth is intuitively obvious, there have been no widescale and large samples of understory sapling growth in relation to light regime. Our second objectives were to determine the importance of light estimation in comparison to other stand characteristics (overstory species, height, basal area, distance to seed source, understory species, densities and site characteristics such as forest floor type, rotten logs, moisture and

nutrient class) as a prediction of early growth of understory white spruce. We use data from a permanent sample plots to test these data.

I)Functions for prediction of crown length and width with tree and stand characteristics.

Methods and Results

Crown height and width are some of the more difficult parameters to obtain in the calibration of the light model. The problem can be broken into three components: tree top height, height to live crown and crown width.

Tree Top Height

Although we initally developed a linear equation for predicting tree top height using the data collected for height to live crown determination (see below), equally good non-linear equations are available in an Alberta Forest Service publication (Huang et al., 1994), and are based on a larger sample size.

These use the Chapman-Richards function, with tree diameter as the sole predictor (Equation 1):

[1] $\text{Height} = 1.3 + a*(1-e^{-b*DBH})^c$

where DBH is the outside bark diameter at breast height and a, b and c are parameters. Parameters are given for each species for the province as a whole, as well as by natural region. R^2 values range from 0.71 to 0.92, except alpine/subalpine lodgepole pine with an R^2 of 0.55.

Height to Live-Crown

A function for determining height to live-crown was obtained using data collected in 23 upland Alberta Forest Service Permanent Sample Plots (PSPs). This set of PSPs contained a wide range of overstory compositions, from aspen to white spruce to lodgepole pine dominated, to mixtures of these species with birch, balsam poplar, black spruce and balsam fir. The plots spanned the central mixedwood region from Drayton Valley to Lac La Biche. Most were 30 x 30 m in size. We measured diameter at breast height (outside the bark at 1.3m; DBH), tree top height (HT), crown width (CW) and height to the base of the live crown (HTLC) in these sites on a subset of trees in each plot. The latter three measurements were made with a measuring tape and clinometer (held at 90° for CW measurement). We also retallied all trees in the plot to check the forest service stand density value. The most recent forest service re-measurement data were used to calculate the basal area of each species. The sample consists of 23 sites with 629 trees. The breakdown by species is 199 aspen, 46 birch, 7 fir, 45 balsam poplar, 81 lodgepole pine, 62 black spruce and 188 white spruce.

Six indicator variables (AWI, BWI, FBI, PBI, PLI, SBI) were constructed for the species effect. These took the values shown below for each species (Table 1). Stepwise regression was used to produce models with reduced numbers of variables, using a probability of 0.2 as the criterion to enter and to stay in the models (PROC REG, SAS System).

Table 1 Class variable SPECIES (indicator matrix) for the summary statistics.

Species	AWI	BWI	FBI	PBI	PLI	SBI
AW (aspen)	1	0	0	0	0	0
BW (birch)	0	1	0	0	0	0
FB (balsam fir)	0	0	1	0	0	0
PB (balsam poplar)	0	0	0	1	0	0
PL (lodgepole pine)	0	0	0	0	1	0
SB (black spruce)	0	0	0	0	0	1
SW (white spruce)	0	0	0	0	0	0

A preliminary analysis suggested that the only useful basal area measurement was the sum of the spruce and fir basal areas (SFBA). This is also meaningful since spruce and fir have crowns that are much more opaque than pine or the deciduous species. If crown recession is controlled by light availability to the lower branches, it makes sense that the presence of these stand-darkening species would raise the base of the live-crown.

We also allowed for two-way interaction effects. These were generated by multiplying variables together, i.e. HTSFBA = HT×SFBA.

The best equation was a relatively simple one, with tree height and species, the plot basal area of spruce + fir (SFBA), and their two-way interactions as predictors of height to crown. R^2 for this model was 0.76. Table 2 shows the other statistics for this equation:

Table 2. Regression Statistics for Height to Live-Crown Equation

SOURCE	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARE	F VALUE	Pr>F
Model	21	13836.19	658.87	92.45	0.0001
Error	607	4326.02	7.13		
Corrected Total	628	18162.21			
HT	1	179.32	179.32	25.16	0.0001
SFBA	1	32.64	32.64	4.58	0.0327
HTSFBA	1	23.37	23.37	3.28	0.0706
SPECIES	6	93.72	15.62	2.19	0.0422
SPECIESHT	6	272.09	45.35	6.36	0.0001
SPECIESSFBA	6	281.10	46.85	6.57	0.0001

PARAMETER	DEGREES OF FREEDOM	ESTIMATE	STANDARD ERROR	T*	Pr>|T|
INTERCEPT	1	-3.424	1.784	-1.92	0.0554
HT	1	0.5477	0.0756	7.24	0.0001
SFBA	1	2.132	0.735	2.90	0.0039
HTSFBA	1	-0.05177	0.02859	-1.81	0.0706
AWI	1	-0.9408	1.7318	-0.54	0.5872
BWI	1	3.736	6.708	0.56	0.5778
FBI	1	1.190	5.819	0.2	0.8381
PBI	1	5.892	2.989	1.97	0.0491
PLI	1	5.001	2.358	2.12	0.0344
SBI	1	-4.922	3.990	-1.26	0.2074
AWIHT	1	0.4172	0.0747	5.58	0.0001
BWIHT	1	-0.0592	0.6685	-0.09	0.9295
FBIHT	1	0.01272	0.34313	0.04	0.9704
PBIHT	1	-0.1217	0.1776	-0.69	0.4933
PLIHT	1	0.1097	0.0923	1.19	0.2349
SBIHT	1	-0.01048	0.15886	-0.07	0.9474
AWISFBA	1	-1.463	0.256	-5.72	0.0001
BWISFBA	1	-1.451	2.631	-0.55	0.5815
FBISFBA	1	-0.5498	2.6274	-0.21	0.8343
PBISFBA	1	0.06752	0.58096	0.12	0.9075
PLISFBA	1	-1.314	0.462	-2.84	0.0046
SBISFBA	1	2.758	2.285	1.21	0.2280

*T value based on the hypothesis that the parameter = 0

The linear equation to predict height to live crown is the sum of the products of each parameter and its corresponding measurements, i.e.

[x] Height to live crown = INTERCEPT +
HT * tree height +
SFBA * spruce&fir basal area +
HTSFBA * tree height * spruce&fir basal area +
AWIHT * tree height +
BWIHT * tree height +
FBIHT * tree height +
PBIHT * tree height +
PLIHT * tree height +
SBIHT * tree height +
AWISFBA * spruce&fir basal area +
BWISFBA * spruce&fir basal area +
FBISFBA * spruce&fir basal area +
PBISFBA * spruce&fir basal area +
PLISFBA * spruce&fir basal area +
SBISFBA * spruce&fir basal area

Crown width

Crown width data collected from the 23 PSPs allowed us to obtain very good regressions for estimation of crown width within plots. When these 23 plots were combined to predict among-plot variation there was very poor estimation. However, we obtained a larger data set from Canadian Forest Products Hines Creek Division which was collected in the Peace River region. This data set had 12,630 individual tree measurements from 946 plots. Crown width was estimated with a measuring tape only (relying on 'eyeballing' to estimate the crown extent). Unless there was a constant bias in this estimate, the large size of the data set should provide a good estimate of the mean relationship.

In these data there are three dominant species, lodgepole pine (7436 measurements), white spruce (2342 measurements), black spruce (1274 measurements) and trembling aspen (1578 measurements). The data were first sorted by plot number then species, then diameter. Every second value was removed from the data set for later validation of the multiple regression model. This ensured that the model would be fit and validated on data covering a similar range of size, species and geographic range. For the purposes of the regression, no distinction was made between within-plot measurements and between plot-measurements, i.e. each data row consisting of plot number, tree species, diameter, height, stand density, stand height was weighted equally regardless of the plot it came from. Three indicator variables (AWI, PLI, SBI) were constructed for the species effect. These took the values shown below for each species.

Species	AWI	PLI	SBI
AW (aspen)	1	0	0
PL (lodgepole pine)	0	1	0
SB (black spruce)	0	0	1
SW (white spruce)	0	0	0

We also allowed for different diameter, height, and density effects for each species (two-way interactions). These were generated by multiplying each indicator variable by each of the continuous predictor variables, i.e. DBHPLI = DBH×PLI. With these 9 interaction terms, there were a possible 16 predictors: AWI, PLI, SBI, DBH, HT, STANDHT, DENSITY, DBHAWI, DBHPLI, DBHSBI, DENAWI, DENPLI, DENSBI, HTAWI, HTPLI, and HTSBI.

A preliminary analysis of the data were done using and the summary statistics of the means are presented in Table 3.

Table 3 Summary statistics for variables used to estimate crown width (half of full data set)

Variable	N	Mean	Std Dev	Minimum	Maximum
AWI	6315	0.1239905	0.3295968	0	1.0000000
PLI	6315	0.5882819	0.4921836	0	1.0000000
SBI	6315	0.1016627	0.3022282	0	1.0000000
DBH	6315	18.4269517	6.6805019	8.5000000	65.2000000
HT	6315	17.9567696	4.3216975	3.5000000	33.8000000
STANDHT	6315	19.8373713	3.3808508	11.0000000	32.0000000
DENSITY	6315	1749.54	738.3790165	100.0672000	4002.69
AWIDBH	6315	2.5995091	7.3311845	0	65.2000000
PLIDBH	6315	10.5961520	9.8578283	0	48.7000000
SBIDBH	6315	1.4538559	4.5163114	0	34.1000000
AWIHT	6315	2.5288044	6.8547049	0	33.8000000
PLIHT	6315	10.5777672	9.2617613	0	32.0000000
SBIHT	6315	1.3690736	4.1931734	0	26.8000000
AWIDEN	6315	189.1215418	543.0189370	0	3302.22
PLIDEN	6315	1081.98	1062.82	0	4002.69
SBIDEN	6315	210.9572757	681.8399810	0	4002.69

All predictor variables were subsequently standardized by subtracting their mean then dividing by their standard deviation ($[x-\mu]/s$). The crown width (CW) data were not standardized.

Table 4 Pearson Correlation Coefficients for crown width and stand variables.

	AWI	PLI	SBI	DBH	HT	DENSITY	STANDHT
CW	0.3234	-0.1874	-0.1304	**0.6756**	0.4953	-0.3830	0.3411
AWI		-0.4497	-0.1266	0.1430	0.2123	-0.1143	0.1482
PLI			-0.4021	-0.0743	0.0066	0.1452	-0.2710
SBI				-0.2078	-0.3495	0.1483	-0.2205
DBH					**0.7925**	-0.4579	0.4830
HT						-0.3611	**0.5538**
DENSITY							-0.5326

With this quantity of data, all correlation coefficients among crown width and stand variables (Table 4) were significant at $p<0.05$. Values larger than 0.5 are highlighted in boldface type. Not surprisingly, tree diameter is well-correlated with tree height and tree height with stand height. Density also has a high negative correlation with stand height as tall stands are less dense.

Fitting the Full Model

Table 5 Analysis of Variance of the linear regression model of crown width in relation to stand characteristics (all 16 standardized predictors included).

Source	DF	Sum of Squares	Mean Square	F Value	Prob>F
Model	16	5617.64001	351.10250	468.691	0.0001
Error	6298	4717.90968	0.74911		
C Total	6314	10335.54968			

Root MSE	0.86551	R-square	0.5435
Dep Mean	2.66743	Adj R-sq	0.5424
C.V.	32.44748		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob > |T|
INTERCEP	1	2.649570	0.01254987	211.123	0.0001
AWI	1	0.281685	0.01584736	17.775	0.0001
PLI	1	-0.030977	0.01671209	-1.854	0.0638
SBI	1	-0.058953	0.02017674	-2.922	0.0035
DBH	1	0.989642	0.02033199	48.674	0.0001
HT	1	-0.181573	0.02112000	-8.597	0.0001
STANDHT	1	-0.018399	0.01593519	-1.155	0.2483
DENSITY	1	-0.072287	0.01397408	-5.173	0.0001
AWIDBH	1	0.036471	0.01957863	1.863	0.0625
PLIDBH	1	0.156653	0.02216617	7.067	0.0001
SBIDBH	1	-0.018218	0.02700921	-0.675	0.5000
AWIDEN	1	0.060839	0.01737998	3.501	0.0005
PLIDEN	1	0.074914	0.01712025	4.376	0.0001
SBIDEN	1	0.019714	0.01349436	1.461	0.1441
AWIHT	1	0.078458	0.02149040	3.651	0.0003
PLIHT	1	0.059708	0.02231366	2.676	0.0075
SBIHT	1	0.009757	0.02253616	0.433	0.6651

Residual/Influence Analysis of the Full Model

We performed an initial analysis of the residuals from the full 16 predictor model (Table 5) to check for evidence of heterogeneous variance, quadratic terms, or a non-normal distribution of residuals. We used studentized residuals since these can be compared directly to the *t* distribution. Although, the data are not shown, we also computed leverage (H), Cook's D, and DFFITS for each observation using SAS to check the amount of influence each point.

The residual plots showed no striking pattern that might indicate a dependence of the variance on the predicted values, diameter, height, density or stand height, nor are there any quadratic trends apparent in the data. There are a number of outlying observations. Four had studentized residuals greater than 5 and 11 had residuals greater than 4. The critical *t* value for 6315 observations and 17 parameters (16 + 1 constant) is $t_{.025, 6298} = 2.24$. The number of observations with residuals greater than this value was 217 out of 6315, or 4.5%. This many outliers might be expected given the size of this data set. The four observations with the largest residuals were large diameter, taller trees in low-density stands of medium stand height (see residual plots). Occasionally, trees with very large crowns are found in low-density stands where their crowns can develop unimpeded and where fire has long been absent. These appear to be such trees.

There is little reason from the point-of-view of the residuals to discard these trees. However, since, they are at the low end of the density range and mid to high-end of the diameter and height range, their influence on the regression parameters and predictions

may be high. We used the DFFITS statistic to check for the influence of these observations, since the Cook's D values reported by SAS were all less than the recommended value ($F_{.5,17,6298}$) of 0.96. There were 370 observations (6% of the total) with DFFITS greater than the recommended value ($2\sqrt{p'/n} = 0.104$). There were six observations in particular that stood out, with DFFITS > 0.48. All other DFFITS were 0.36 or less, and decreased gradually toward zero. Since the only reason for removing data would be to restrict the regression to fit the 'typical' response, we deleted these six observations with large DFFITS. Three of these observations had the highest leverage values and the other three had the highest PRESS statistics. It seemed that these six are indeed, true 'outliers' and worth removing.

Table 6 Analysis of variance of the linear regression model of crown width in relation to stand characteristics (Outliers Removed)

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Prob>F
Model	16	5659.86722	353.74170	480.828	0.0001
Error	6292	4628.97592	0.73569		
C Total	6308	10288.84314			

Root MSE	0.85773	R-square	0.5501
Dep Mean	2.66684	Adj R-sq	0.5490
C.V.	32.16259		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob > |T|
INTERCEP	1	2.652164	0.01244226	213.158	0.0001
AWI	1	0.287191	0.01574270	18.243	0.0001
PLI	1	-0.030813	0.01656918	-1.860	0.0630
SBI	1	-0.058954	0.01999715	-2.948	0.0032
DBH	1	1.008489	0.02028206	49.723	0.0001
HT	1	-0.196148	0.02101368	-9.334	0.0001
STANDHT	1	-0.015140	0.01582385	-0.957	0.3387
DENSITY	1	-0.070550	0.01386558	-5.088	0.0001
AWIDBH	1	0.050436	0.02010705	2.508	0.0122
PLIDBH	1	0.135686	0.02230197	6.084	0.0001
SBIDBH	1	-0.031166	0.02687033	-1.160	0.2462
AWIDEN	1	0.058475	0.01726615	3.387	0.0007
PLIDEN	1	0.072260	0.01699673	4.251	0.0001
SBIDEN	1	0.018122	0.01338753	1.354	0.1759
AWIHT	1	0.070281	0.02158952	3.255	0.0011
PLIHT	1	0.075050	0.02228257	3.368	0.0008
SBIHT	1	0.019326	0.02239644	0.863	0.3882

The model with the six outliers removed (Table 6) has a slightly better R^2 than the model fit to the whole dataset (0.5501 vs. 5435) as might be expected by removing outlying data. Since all predictors are included, this model explains the most variation in crown width possible with this data set.

The best, smallest model contains the species, diameter and height information (Table 7). Adding stand density caused a minor improvement in the fit. The stand height estimate, with its obvious correlation with tree height, was one of the last variables added or first subtracted from the model. We elected to use the species, diameter, height and stand density variables to predict crown width. This provides an R^2 of 0.55. Other statistics and parameter estimates are shown below.

Table 7 Analysis of Variance of the regression model of crown width in relation to stand characteristics (simplest model).

Source	DF	Sum of Squares	Mean Square	F Value	Prob>F
Model	15	5654.81232	376.987488	512.427	0.0001
Error	6292	4628.97592	0.73569		
C Total	6308	10283.78824			

Root MSE	0.85773	R-square	0.5500
Dep Mean	2.66684	Adj R-sq	0.5489
C.V.	32.16259		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	T for H0: Parameter=0	Prob > |T|
INTERCEP	1	2.652164	0.01244226	213.158	0.0001
AWI	1	0.287191	0.01574270	18.243	0.0001
PLI	1	-0.030813	0.01656918	-1.860	0.0630
SBI	1	-0.058954	0.01999715	-2.948	0.0032
DBH	1	1.008489	0.02028206	49.723	0.0001
HT	1	-0.196148	0.02101368	-9.334	0.0001
DENSITY	1	-0.070550	0.01386558	-5.088	0.0001
AWIDBH	1	0.050436	0.02010705	2.508	0.0122
PLIDBH	1	0.135686	0.02230197	6.084	0.0001
SBIDBH	1	-0.031166	0.02687033	-1.160	0.2462
AWIDEN	1	0.058475	0.01726615	3.387	0.0007
PLIDEN	1	0.072260	0.01699673	4.251	0.0001
SBIDEN	1	0.018122	0.01338753	1.354	0.1759
AWIHT	1	0.070281	0.02158952	3.255	0.0011
PLIHT	1	0.075050	0.02228257	3.368	0.0008
SBIHT	1	0.019326	0.02239644	0.863	0.3882

Since the parameter estimates given above are for standardized data ($[x - \mu]/s$), the parameter estimates were recalculated for use with raw data. The predictive equation for raw data is:

Crown width = 1.061
+ 0.145*AWI
+ 0.144*SBI
+ 0.1248*DBH
- 0.0414*HT
- 0.0000153*DENSITY
+ 0.0236*AWI*DBH + 0.0394*PLI*DBH
+ 0.000145*AWI*DENSITY
- 0.000149*PLI*DENSITY
- 0.000110*SBI*DENSITY
+ 0.0154*AWI*HT
- 0.0272*PLI*HT

where AWI, SBI and PLI are species indicator variables as shown above.

We used this model to predict the crown width of the other 6315 trees which were withdrawn from the calibration data set. The mean bias of the model (predicted minus measured crown width), using this validation data, is 0.002 m with a standard error of 0.902, so the mean bias is not significantly different from zero (P=0.8634). There is no bias in the model for predicting crown widths measured in this fashion.

Discussion

The equations developed above can be used to take inventory data and estimate the crown characteristics of individual trees. The equations can therefore be a fundamental component of the calibration of the MIXLIGHT model. The ability to predict crown length from stand level data that might be collected in a normal inventory were much

stronger than the ability to predict crown width. This is unfortunate for light modelling as the previous sensitivity analysis of the MIXLIGHT model (Stadt and Lieffers 1998) indicated that crown width is a more important variable for the model than crown length especially if crown width is overestimated. We have several theories about the poorer estimation of crown width. Crown width data were estimated on individual trees using the relatively imprecision in visual estimation of the crown width. There likely was significant error in this technique, especially between observers. Secondly, since our preliminary within-plot regression models of crown width in relation to tree were much better (R^2>0.70 for within plot compared to R^2 =0.55 for the overall data set), there must be some site property causing this variation. Part of this may relate to differences in crown friction (Putz et al. 1984, Long and Smith 1992) related to differences in average wind speeds or stem stiffness (related to taper) between sites. Crown friction has been shown to be important factors controlling branch and foliage loss (Grier 1988). It may be some time before these processes can be adequately predicted.

II) Using MIXLIGHT stand-level light estimates as predictors of understory white spruce growth

The objective of this section was to use light estimation and other stand variables as predictors of understory spruce growth rates.

Methods

The above estimators of crown length and crown width were used to estimate the crown volumes and then the leaf area of stands using the stand-level module of the MIXLIGHT model. The model was applied to data from 50 Permanent Sample Plots (PSPs) established by the Forest Branch of the Alberta Lands and Forest Service. Supplementary data were collected on spruce understory from the same PSPs.

Data were obtained from PSPs falling into the submesic to hygric ecological moisture classes and the submesotrophic to permesotrophic ecological nutrient classes were selected from the Boreal Mixedwood and Lower Boreal Foothills ecoregions (Anonymous, 1993).

Data in the Forest Service data base was collected according to the procedures detailed in the Permanent Sample Plot Field Procedures Manual (Anonymous, 1993), and the Ecological Land Classification Manual (Anonymous, 1994). The PSPs were restricted to the more recent type where there was one plot, measuring approximately 30 × 30 m. In each, all standing trees were identified by species and measured for diameter at 1.3 m. Understory vegetation was recorded by species and percent cover (vertical projected area). Soil type and texture were determined from pits, and nutrient and moisture classes were identified.

In each of the sites, existing data was verified where possible, and a transect survey run through the site. The transect was triangular, 30 m on a side, and centred on the plot centre. On each leg of the transect, the total height, height increment of the previous

three years, and establishment substrate of the first 10 white spruce regeneration (<3 m tall) were collected. Measuring more than 3 seedlings from a cluster on a single substrate was avoided where possible. Tallies of white spruce regeneration (<3 m tall) were made for each leg. The diameter, length of the intersection with the transect, species, and rot class of coarse woody debris (>10 cm diameter where it crossed the transect) were also measured. Coarse woody debris was classified into one of six rot classes based on field identifiable characteristics (modified from Sollins et al., 1987). The rot classes were: 1) Newly fallen, with twigs and bark mostly intact. 2) Twigs gone; bark and branches present but deteriorating. Wood mostly sound. 3) Most branches missing, bark sloughing off, outer wood decaying, but still dimensionally stable. Some bryophyte colonization. 4) Bark and branches gone, branch stubs easily removed. Outer wood decayed, inner wood still hard. Colonized by bryophytes and vascular plants. 5) Inner wood decayed, bole collapsing; mostly colonized and contiguous with forest floor vegetation. 6) Completely collapsed and hidden beneath forest floor. With 2 exceptions, the wood on which seedlings were growing was of rot class 4 or greater; therefore, our calculations of rotten wood coverage included only these classes. Mineral soil cover was estimated from the proportion of the transect that intersected it. The depth of the forest floor (LFH layers) was measured in three places. A description of the variables used in this study are presented in Table 8.

Data manipulation

For each PSP, we calculated the total basal area per hectare for each canopy tree species, and the total basal area for each sapling tree species. Soil percent clay and sand values were calculated from textural classes using average values for the different classes

(Canada Soil Survey Committee, Subcommittee on Soil Classification, 1978). Since the regenerating white spruce trees will overtop successive layers of competing understory vegetation, we calculated mean 3-year height increments for seedlings of four different height strata: 0-20 cm, 20-50 cm, 50-150 cm and 150-300 cm. For each height 'cohort' the 3-year mean height increment was averaged across the plot (MEAN3I).

As a preliminary analysis, bivariate correlations were calculated between all variables and the light transmission estimate and between all variables and the mean 3-year height increments (MEAN3I) of the seedling white spruce (Table 8). Indicator variables were constructed for ecological nutrient and moisture regimes as follows.

Ecological nutrient regime	NUTR1	NUTR2
submesotrophic	0	0
mesotrophic	1	0
permesotrophic	0	1

Ecological moisture regime	WATER1	WATER2	WATER3
Submesic	0	0	0
Mesic	1	0	0
Subhygric	0	1	0
Hygric	0	0	1

Regression analysis

Data from the 50 PSPs containing white spruce regeneration were used to build regression models predicting white spruce seedling height increment. Stepwise regression was used to produce models with reduced numbers of variables, using a probability of 0.2 as the criterion to enter and to stay in the models (PROC REG, SAS System).

Results

Table 8. Variables used to predict white spruce height growth and their correlation with light and seedling height increment. ND = no data. Significant correlations ($P>0.05$) are highlighted in bold (n = 34 to 39).

Variable	Description	Correlation with light	Correlation with white spruce mean 3-year height increment			
			0-20 cm trees	20-50 cm trees	50-150 cm trees	150-300 cm trees
LIGHT	MIXLIGHT overstory light transmission estimate	1.00	-0.05	0.09	-0.03	0.03
ELEV	elevation (m)	-0.19	**-0.39**	-0.23	-0.19	-0.19
STANDAGE	years since disturbance	**0.46**	0.18	-0.15	0.16	0.03
MF_COVER	% feather moss cover	**-0.53**	-0.21	**-0.37**	**-0.38**	**-0.35**
MO_COVER	% other moss species cover	**-0.40**	-0.11	0.15	0.25	0.03
LICHCOVR	% lichen cover	0.02	**-0.34**	0.03	-0.30	**-0.39**
HUM_DEP	humus depth (cm)	-0.15	-0.03	-0.31	-0.13	-0.18
WATER1*	ecological moisture class	0.16	-0.09	-0.13	-0.01	-0.04
WATER2*	ecological moisture class	0.02	-0.03	0.04	0.09	0.17
WATER3*	ecological moisture class	0.01	0.13	0.14	-0.03	-0.15
NUTR1**	ecological nutrient class	-0.02	-0.03	-0.07	-0.14	-0.16
NUTR2**	ecological nutrient class	0.15	-0.07	0.02	0.16	**0.38**
PCT_CLAY	soil clay fraction (%)	-0.04	-0.22	-0.20	-0.21	-0.26
PCT_SAND	soil sand fraction (%)	0.19	0.01	-0.03	-0.01	0.13
AWTREEBA	aspen tree basal area (m^2)	0.20	0.29	0.07	**0.51**	**0.52**
PBTREEBA	balsam poplar tree basal area (m^2)	**-0.34**	0.13	-0.04	0.19	0.26
BWTREEBA	birch tree basal area (m^2)	-0.12	-0.17	**0.41**	0.14	-0.01
PJTREEBA	jack pine tree basal area (m^2)	0.07	-0.17	-0.18	-0.20	-0.10
PLTREEBA	lodgepole pine tree basal area (m^2)	0.25	0.04	0.09	-0.07	0.16
FBTREEBA	balsam fir tree basal area (m^2)	ND	-0.23	0.28	ND	ND
SWTREEBA	white spruce tree basal area (m^2)	**-0.56**	-0.06	-0.28	-0.26	**-0.33**
SBTREEBA	black spruce tree basal area (m^2)	**-0.41**	0.20	0.05	-0.17	-0.03
AWSPLGBA	aspen sapling basal area (m^2)	0.32	-0.13	**0.38**	0.01	0.14
PBSPLBA	balsam poplar sapling basal area (m^2)	0.09	-0.16	0.04	0.03	0.25
BWSPLGBA	birch sapling basal area (m^2)	-0.08	0.27	**0.36**	0.14	0
PJSPLGBA	jack pine sapling basal area (m^2)	**0.40**	-0.10	-0.18	ND	-0.03
SWSPLGBA	white spruce sapling basal area (m^2)	0.29	-0.31	0.20	-0.06	0.11
ALDERCOV	% alder cover	**0.40**	0.02	0.10	0.17	0.17
WILWCOV	% willow cover	0.06	0.21	-0.09	0.15	-0.08
HAZLCOV	% hazel cover	-0.26	-0.03	0.30	**0.58**	**0.47**
FORBCOV	% forb cover	**-0.38**	**0.38**	-0.30	-0.13	-0.26
GRASSCOV	% grass cover	0.04	0.19	-0.07	0.08	-0.07

Light was a poor predictor of white spruce seedling growth. Bivariate correlation of height growth with predicted light transmission was not significantly different from zero for all size classes (Table 8). For the taller white spruce (>50 cm), overstory aspen basal area, hazel cover, and lichen cover were the strongest predictors. Five parameter models were chosen for each size class of the spruce understory. These are shown in Tables 9 below.

Table 9 Prediction of understory spruce height increment for four different height classes.

a) 0-20cm trees

Source	DF	Sum of Squares	Mean Square	F	Prob>F
Regression	5	138.41655020	27.68331004	10.38	0.0001
Error	29	77.36609119	2.66779625		
Total	34	215.78264139		R-square = 0.64146286	

Variable	Parameter Estimate	Standard Error	Type II Sum of Squares	F	Prob>F
INTERCEP	9.47862860	1.21441917	162.51986163	60.92	0.0001
ELEV	-0.01019410	0.00222166	56.16887631	21.05	0.0001
SBTREEBA	2.43586626	0.83738234	22.57417775	8.46	0.0069
SWSPLGBA	-0.22078073	0.14458843	6.22025067	2.33	0.1376
FORBCOVR	0.08291635	0.01666138	66.07104184	24.77	0.0001
MF_COVER	-0.01929968	0.00931631	11.44892413	4.29	0.0473

b) 20-50cm trees

Source	DF	Sum of Squares	Mean Square	F	Prob>F
Regression	5	258.85802190	51.77160438	7.66	0.0001
Error	30	202.74239068	6.75807969		
Total	35	461.60041258		R-square = 0.56078377	

Variable	Parameter Estimate	Standard Error	Type II Sum of Squares	F	Prob>F
INTERCEP	12.53403420	2.02248247	259.55866273	38.41	0.0001
ELEV	-0.00647918	0.00321306	27.48061070	4.07	0.0528
BWTREEBA	0.54258081	0.15970560	78.00310135	11.54	0.0019
FBTREEBA	0.76464173	0.46764592	18.06778889	2.67	0.1125
AWSPLGBA	0.18579869	0.05057655	91.20322013	13.50	0.0009
HAZLCOVR	2.27860204	0.87962725	45.34850018	6.71	0.0147

c) 50-150cm trees

Source	DF	Sum of Squares	Mean Square	F	Prob>F
Regression	4	628.65134028	157.16283507	11.94	0.0001
Error	33	434.54755675	13.16810778		
Total	37	1063.19889704		R-square = 0.59128291	

Variable	Parameter Estimate	Standard Error	Type II Sum of Squares	F	Prob>F
INTERCEP	13.82398240	1.34905723	1382.70320741	105.00	0.0001
AWTREEBA	0.20429383	0.06751164	120.58034497	9.16	0.0048
BWSPLGBA	0.35349653	0.17753063	52.20920405	3.96	0.0548
LICHCOVR	-0.85113641	0.43176408	51.17156453	3.89	0.0571
HAZLCOVR	2.02924837	0.45142467	266.08672342	20.21	0.0001

d) 150-300cm

Source	DF	Sum of Squares	Mean Square	F	Prob>F
Regression	5	2853.86635382	570.77327076	8.18	0.0001
Error	26	1814.77055434	69.79886747		
Total	31	4668.63690816		R-square = 0.61128471	

Variable	Parameter Estimate	Standard Error	Type II Sum of Squares	F	Prob>F
INTERCEP	25.99847282	3.88482542	3126.08684291	44.79	0.0001
AWTREEBA	0.34709542	0.16832583	296.78681653	4.25	0.0493
SWSPLGBA	1.38906329	0.70762353	268.96013564	3.85	0.0604
GRASCOVR	-0.10428386	0.06933969	157.87695891	2.26	0.1446
LICHCOVR	-5.00808426	1.42298290	864.55428913	12.39	0.0016
HAZLCOVR	3.97621302	1.11729232	884.00359855	12.67	0.0015

Discussion

Surprisingly, light was not a strong predictor of understory spruce growth. Spruce seedling growth was better predicted by variables such as overstory basal area, particularly the amount of spruce overstory or understory basal area or grass or lichen cover. Light transmission values were negatively correlated with the conifer basal area and may have been included in the model indirectly through these variables. Other important variables in the models were grass and lichen cover. These were negatively correlated with the understory spruce growth. Grass may have insulated the soil slowing growth while lichens may have been indicators of lower site nutrition. The positive association with hazel cover is likely related to the positive nutrient conditions that also support heavier hazel cover.

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Predicting and managing light in the understory of boreal forests

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The study on which this report is based was partially funded by the Manning Diversified Research Trust Fund (MDRTF). The views, statements and conclusions expressed expressed and the recommendations made in this report are entirely those of the authors and should not be construed as the statements or conclusions of or as expressing the opinions of the MDRFT Committee.

Predicting and managing light in the understory of boreal forests.

By

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., and Comeau, P.G.

This paper reviews current information relating to the dynamics of light in northern and boreal forests, and discusses factors affecting overstory light transmission, seasonality of light, sunflecks, canopy gaps and understory development, particularly with regard to tree regeneration. Techniques for measurement of light in forests such as radiometers, photosensitive paper or chemicals, hemispherical canopy photographs, the plant canopy analyzer or visual estimators of canopy density, are each discussed in terms of their accuracy, costs, ease of use and conditions required during measurement. Predictive models of light transmission based on canopy architecture are also described in terms of their assumptions, accuracy and input data costs. Lastly the paper discusses the relationship among overstory and understory densities, ground level light and "windows of opportunity" for regeneration of trees in the understory following management interventions.

Acknowledgments:

This study was supported with operating grants from the Manning Diversified Research Trust Fund, NSERC, the NCE in Sustainable Forest Management. The authors would like to thank R. Chazdon and the graduate students of VJL and CM for their input into this work.

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Figure caption:

Fig. 1. a) The effect of gap position on seasonally-integrated light transmission. This gap is 24 m wide in a homogeneous birch stand 10 m in height (Comeau et al. 1998). b) The effect of gap size on seasonally-integrated light transmission at gap center (Comeau et al. 1998).

Fig. 2 Idealized relationships between R:FR and PPFD under coniferous vs. deciduous dominated stands under completely sunny or cloudy conditions. The lines drawn for coniferous stands under sunny and cloudy conditions are based on data from Messier & Puttonen (1995) under pure Scots pine stands in Finland and on data points (*) from Messier et al. (1989) under pure stands of western hemlock and western red cedar. These relationships were also checked with data from Ross et al. (1986), Ritchie (1997) and Mailly & Kimmins (1997). The line for deciduous stands under sunny conditions is based on continuous data points covering the range from 1 to 100% full sunlight collected under pure stands of broad-leaf maple in Coastal B.C. by Gendron (Unpublished), and data from Messier & Bellefleur (1988), Morgan & Smith (1981), St-Jacques & Bellefleur (1993), Endler (1993) and Lei et al (1998). The line for deciduous stands under cloudy conditions is based on data from Messier & Bellefleur (1988), Morgan & Smith (1981), Endler (1993) and Lei et al. (1998).

Fig. 3. Pictorial representation of the light transmission models. The actual canopy structure is shown in light gray. The medium-gray area in each frame is the light-absorbing region, which can be canopy (a, b), crown (c, d, e), shoot (e), leaf (e), or layer (f). The sources of light are shown above each canopy: the sun (radiating globe), skylight (stippled bar), or "seasonal sky" (stippled bar with the solar track; see text). Paths taken by light from these sources through the canopy are shown by arrows: the wide arrow represents the path taken by direct sunlight, the narrow arrows are diffuse skylight. Where the "seasonal sky" is the light source, medium arrows are used. Arrows are black where they pass through the models' light-absorbing regions. "Z" is the zenith angle.

Fig. 4. Understory canopy of an intact dense conifer stand 2a, immediately after thinning 2b and five years later 2c. The dense overstory virtually eliminates the understory. The period after thinning allow increased light to ground level but this period is short-lived as the understory eventually colonizes this space.

Fig. 5. Understory canopy of a mature aspen stand 3a, immediately after strip understory site preparation 3b, and five years later 3c. The porous overstory of the aspen allows a heavy understory to develop. The strip site preparation provides a temporary increase in light to ground level but the understory eventually redevelops.

Introduction

Photosynthetically active radiation (PAR), i.e., between 380 and 710 nm (Larcher 1980), is fundamental for photosynthesis and growth of understory plants (Canham et al. 1990, Sims and Pearcy 1993, Chen and Klinka 1997). While other spectral bands are important for the thermal environment in the forest understory (Bunnell and Vales 1990, Black et al. 1991), this review focuses on visible light (380-770 nm) and PAR, which owing to the similarity of their spectral range, are often used synonymously. Stand density and light interception (Goetz and Prince 1996) are the critical factors controlling the stages of forest stand development and the establishment of saplings in the understory of forests (Oliver and Larson 1990) and are the variables most often considered in predicting establishment and growth of regeneration following partial cutting (Nyland 1996; Smith et al 1997).

A synthesis of the large body of literature on light dynamics in forest stands is timely given the renewed interest in partial-cut silvicultural systems, management of mixed species stands and the desire to establish trees in partial shade. We review issues related to light in boreal and northern forests, especially in regards to conditions for the establishment and growth of tree seedlings. These high latitude sites (i.e. > 45°) are characterized by short summers with relatively low maximum solar elevations and long winters with very low solar elevations. This paper describes canopy level and microsite level light regimes and the techniques for measuring and estimating light at each of these scales. We review the dynamics of overstory light transmission diurnally, annually and during stand development; the spatial heterogeneity and spectral quality of light; the interception of light by understory shrub and herb layers; the different techniques for measuring light and simulation models for prediction of light; and lastly, the application of this knowledge to the management of forests and directions for future work.

Dynamics of Light in Forests

Overstory light transmission

Light in forests is constantly changing in both intensity and direction (Anderson 1964, Norman and Jarvis 1975, Gay et al. 1971, Baldocchi and Collineau 1994) because of the earth's daily and annual celestial movements relative to the position of the sun. The apparent

path of the sun relative to a position on the earth's surface can be described geometrically in relation to season and time of day (Duffie and Beckman 1974). These differences and the constant change in cloud cover result in a wide variation in incoming light above forest stands. When tree, shrub and herb canopies of various size, shape and opaqueness are present on a site, the amount of light penetrating the canopy is further changed.

Diffuse light, which emanates from other parts of the sky as a result of scattering of sunlight by the atmosphere, varies in significance with latitude, angle from the horizon, cloud cover and pollution. The forward scatter of light striking aerosols in the atmosphere can increase the amount of diffuse light on days when the sky is not completely clear (Monteith and Unsworth, 1990). This same effect causes a 5 to 10 % increase in total light on days with broken cumulus clouds, during the times when the sun is not covered by cloud (Monteith and Unsworth, 1990). While there are some differences in the amount of diffuse light emanating from various parts of the sky (Grant, 1985; Wang and Jarvis 1990), for simplicity it is commonly assumed that each sector of the sky dome is uniformly luminous (Canham et al. 1994). On days with complete cloud cover, the hemispheric origin of the light means that there is much less spatial and temporal variation in light within the forest (Messier and Puttonen 1995, Parent and Messier 1996). In addition to light coming directly from the sky, some photosynthetically active radiation passes through the leaves themselves or is reflected downward by the foliage. On clear days, scattering of sunlight by this process is called beam enrichment (Hutchison and Matt 1976) and can represent 15% of midday radiation coming through the overstory and 40% of radiation below the shrub layer (Hutchison and Matt 1976) in deciduous stands or 14 to 41% of the overstory transmission for hardwood or conifer-dominated stands (Canham et al. 1994). Others (Gay et al. 1971, Vales and Bunnell 1988a) have inferred beam enrichment from an increase in the proportion of diffuse light under the canopy compared to the proportion above, but this may be confounded by the differential absorption of diffuse light relative to direct light, which depends on the inclination of foliage and sun angle even in the absence of scattering (Oker-Blom 1986).

Seasonality of Light

Seasonal differences in canopy light transmission are driven by differences in solar elevation, day length and phenology of the vegetation (Hutchison and Matt 1977, Uemura 1994). Because some broadleaf trees carry foliage only in the summer, their effect on reducing the percentage of above canopy light is highest in summer (Hutchison and Matt 1977, Constabel and Lieffers 1996). There are also seasonal differences in boreal spruces and pines of 5 to 10% because of timing of needle flush and cast (Chen 1996). Measurement of light in spring and fall is important because some evergreen species in the understory may be able to photosynthesize during the periods when the hardwoods are leafless; indeed Emmingham and Waring (1977) estimated 50% of the annual photosynthesis of conifers in the Pacific Northwest occurs between October and May. In the cold winters of the boreal forest, evergreen species are not photosynthetically active (Jurik et al. 1988, Man and Lieffers 1998). The periods of hardwood leaf-off in April and early May and in late September and October, however, are also important for photosynthesis of understory white spruce (Man and Lieffers 1997) and evergreen boreal forests herbs (Landhaüsser et al. 1997). Also, while light in the winter months may not be directly important for photosynthesis, bright light in conjunction with freezing temperature may damage photosystem II (Lundmark and Hällgren 1987).

Canopy Gaps, Sunflecks and Spatial Heterogeneity

Large gaps in the canopy permit long periods of uninterrupted transmission of direct beam light to the understory (e.g. Runkle 1981, Canham 1988, Canham et al. 1990). Canopy gaps create a range of light conditions within and around the gap opening depending upon the sun angle, tree height and sky condition (Canham et al. 1990, Messier 1996). As the size of an opening increases, the amount of light reaching the center of the gap also increases as a function of both the diameter of the gap (Fig. 1b) and the height of the surrounding stand, i.e., the sky view factor. At night, the sky view factor is related to radiation loss to the sky and the occurrence of summer frosts (Groot and Carlson 1996).

Even in relatively uniform stands with a relatively dense overstory, there is significant spatial variation in light transmitted to the understory. Hutchison and Matt (1977), Kikuzawa (1992) and Messier et al. (1998) note a positively-skewed distribution of light in the understory, presumably because of similar variation in overstory structure. Thus, even in stands with few apparent canopy gaps, there are some understory positions with higher light regimes where

seedlings could be established. At present there is a shortage of information on the range of light regimes in understory and its effects on forest dynamics.

In high latitude sites, because of the low solar elevation, the location of high radiation at the ground level is offset relative to the gap centre (Canham 1988, Canham et al. 1990, Dai 1996). Thus, in the northern hemisphere, the south edge of a forest opening will receive diffuse light from the northern portion of the sky, while the northern edge of the gap will receive both diffuse and direct beam light (Canham et al. 1990, Bazazz and Wayne 1994) (Fig. 1a). At high latitudes and if trees are tall, the effectiveness of the small to moderate-sized gaps for creating regeneration habitats may be compromised as the area of increased light does not coincide with the area of reduced competition for water and nutrients. Given that most boreal forest species have relatively narrow crowns (Kuuluvainen and Pukkala 1989), once gaps are created, further growth of crowns is less likely to close the canopy gaps. In eastern deciduous forests, by comparison, crown expansion into gaps is an important factor (Runkle 1981; Hibbs 1982; Runkle and Yetter 1987; Valverde and Silvertown 1997).

Sunflecks can be defined as a small patch on the forest floor that on a sunny day receives a substantial increase in the amount of direct beam light relative to the general forest floor (Chazdon 1988). As some canopies transmit much more light than others, the application of the above qualitative definition results in a range of thresholds for sunflecks (Table 1). Unfortunately, different choices of threshold result in different estimates of the importance of sunflecks, making it difficult to distinguish between the effects of different thresholds and real differences in sunfleck importance. To illustrate this, Messier et al. (1998) found a sunfleck contribution of 60 to 86% of daily PAR using a 100 $\mu mol\ m^{-2}\ s^{-1}$ threshold and 28 to 75% with a 250 $\mu mol\ m^{-2}\ s^{-1}$ threshold over a full sunny day in mid-summer in closed boreal forest stands (Table 1) . Logically, it might be better to select sunfleck thresholds that are related to the photosynthetic light response curve of important understory plants. We also suggest that it is most appropriate to estimate the importance of sunflecks over at least one full range of daylight hours on completely clear. Other studies have estimated that sunflecks contribute anywhere from 32-90% of daily PAR (Table 1) but these estimates are subject to the concerns raised above.

Sunflecks resulting from small concrete canopy openings are of relatively short duration and relatively low intensity because of penumbral effects. The penumbral effect is related to the fact that direct beam radiation is not from a point source, i.e., the solar disc and aureolus has area. At a distance 50 to 70 times the diameter of the opening in the canopy, the centre of the sunfleck drops below full light intensity and the opening is entirely penumbra (Horn 1971; Smith et al. 1989; Oliver and Larson 1990). Smith et al. (1989) suggests to use this ratio (gap size/distance to the incident opening) to differentiate among sunflecks (<0.01), sunpatches (>0.01 but <0.05), gaps (>0.05 but < 1.0) and clearings (>1.0). Thus many small openings in the canopy of tall trees will result in a relatively uniform and diffuse light at ground level. This has been described as high shade (Chapman 1944). Tree seedlings in high shade are known to loose epinastic control of terminal buds resulting in a shrub-like form of trees in deeper shade (Oliver and Larson 1990). The mechanism for this is not clear but it may relate to the uniform intensity of the light as much as to the low total daily irradiance (Oliver and Larson 1990) or the modifications in the quality of light beneath large vs. small canopy holes (Endler 1993).

The uniformity of light plays a role in seedling development. An environment of uniform but moderate shade produces larger seedlings than an environment with lower light for most of the time but with periods of high light due to sunflecks, even though the daily total irradiance was the same (Wayne and Bazzaz 1993, Sims and Pearcy 1993). In essence, the periods of very strong light cannot be fully used, as the light levels exceed the linear quantum yield portion of the light-response curve (Sims and Percy 1993). Secondly, in some forests sunflecks may have a median duration as short as 2 seconds (Chazdon and Percy 1991). To take advantage of these brief periods of higher light, the photosynthetic system of plants must be induced by recent exposure to strong light. This may take as long as 20 to 60 minutes (Chazdon and Percy 1991), although in Douglas fir, 90% induction of understory-adapted trees may occur in as little as 63 seconds (Chen and Klinka 1997). For shade leaves, especially of late successional species, induction can be maintained by a series of light pulses (Küppers et al. 1996). In many woody species, stomata remain open during short periods of low light, while in many herbaceous species, stomata track light levels, closing during periods

of low light and opening rapidly in response to high light (Knapp and Smith 1990). Given the variation in understory environments within and among stands there is opportunity for development of specialists to exploit these light environments. However, because the boreal forest is a relatively young (<12,000 years) community (Ritchie 1978), species with specialized physiological strategies may not have had time to develop. For example, *Calamagrostis canadensis* is able to survive in aspen understories but will close its stomata during brief dark periods and requires 2 minutes of strong light induction to begin reopening them (Greenway and Lieffers 1997), thus it is not particularly well-suited to take advantage of brief sunflecks.

Light Quality

Forest canopies absorb or reflect much of the photosynthetically active radiation while transmitting most of the far-red part of the spectrum (ca. 730 nm) (Larcher 1980). Different canopy structures result in differences in the quality of transmitted light (Endler 1993); in sunny conditions, light under a full canopy is yellow to green, small sunflecks are dominant in the red part of the spectrum, while large gaps produce white light (Endler 1993, Turnbull and Yates, 1993). One of the most common ways of summarizing spectral quality is the red:far-red ratio, i.e. the ratio between transmitted light in the red band (655-665 nm) to far-red light (725-735 nm) (Larcher 1980). In general, the R:FR ratio declines with increasing canopy density (Messier et al. 1989). On sunny days this decline is steeper than on cloudy days (Endler 1993; Messier and Puttonen, 1995). This has been noted for hardwood stands (Messier and Bellefleur 1988), Scots pine (Messier and Puttonen 1995), radiata pine (Morgan et al. 1985) and mixed conifers (Federer and Tanner 1966). On sunny days, the R:FR ratio may vary from 0.1 under dense eastern hardwoods (Messier and Bellefleur 1988) to 1.0 in large gaps (Turnbull and Yates 1993; Lei et al. 1998), and from 0.4 under dense conifer canopies to 1.0 in large gaps (Messier et al. 1989; Messier & Puttonen, 1995; Ritchie, 1997; Mailly et al. 1997). Generally, hardwood canopies have a lower R:FR ratios than conifer canopies (Ross et al. 1986, Messier and Bellefleur 1988, Messier et al. 1989, Messier and Puttonen 1995) suggesting better absorption of red light by hardwoods. Fig. 2 summarizes these observations and proposes idealised relationships for both pure deciduous and coniferous species on both completely sunny and cloudy days.

While plants have photoreceptors specific for ultraviolet and blue radiation (Aphalo and Ballaré 1995) the most common mechanism by which plants respond to changes in light quality is through the phytochrome system (Smith 1982) which is influenced by the R:FR ratio (Larcher 1980). Seed germination, stomatal opening and leaf and stem morphology of many plant species are affected by this ratio (Smith 1982, Endler 1993), but trees that are commonly found in understory conditions (Smith 1982; Bazzaz and Wayne 1994; Kitajima, 1994; Lee et al. 1996) are less likely to respond to changes in the R:FR ratio. Light quantity alone, however, seems to have a much more pronounced effect on tree growth and physiological acclimation to shade than light quality (Kitajima, 1994: Lee et al. 1996).

Light in relation to stand development

As a stand reaches crown closure, i.e. the stem exclusion phase (Oliver and Larson 1990), light transmission to the understory declines sharply. After this stage there is an increase in overstory light transmission: for aspen (Lieffers and Stadt, 1994, Constabel and Lieffers 1996), Scots pine (Messier and Puttonen 1995) and eastern hardwoods (Brown and Parker 1994) as leaf area declines with age. Aspen stands in Minnesota, however, did not show a decline in leaf area with age up to ca. 100 years (Woods et al. 1991, Goetz and Prince 1996). In spruce-aspen mixedwoods, the higher the percentage composition of spruce in the overstory the less light is transmitted to the understory (Lieffers and Stadt, 1994, Constabel and Lieffers 1996). Constabel (1995) noted that light transmission through the crowns of single spruce trees was one-half to one-tenth that of aspen trees of similar stem size. Canham et al (1994) and Messier et al. (1998) also observed that shade intolerant species (either deciduous or coniferous) transmit more light than shade tolerant species presumably because of a thinner crown.

The ability of trees to support leaf area and thus intercept light decreases with environmental stress (Waring and Schlesinger 1985). Aspen stands in Quebec, therefore transmit less light than the same stand types in Alberta possibly because of the greater annual precipitation in eastern forests (Messier et al. 1998). In general, light transmission is higher for boreal forests with their cold conditions than for the warmer and wetter temperate deciduous forests

(Messier and Bellefleur 1988; Canham et al. 1990, Brown and Parker 1994) or conifer forests of the pacific northwest (Messier et al. 1989). Messier (1996), found in closed boreal forests that light transmission above the shrub layer varies from 2 to 40%, whereas in temperate and coastal forests it is usually less than 5%.

Light transmission through shrub and herb layers

The effect of shrubs and herbs on the light regime at the ground level is also important as this is where seedlings must start their life. Germination of seedlings on elevated microsites such as on rotten logs or mounds (DeLong et al. 1998) elevates seedlings above some of the shading by the herbaceous layer and may improve their growth and survival. Tree seedlings gradually grow up through the shrub and herb layers, thereby overtopping this shading leaf area and improving their prospects. Minimum light levels required for survival, however, may also increase as a sapling becomes larger (Givnish 1988; Messier 1996).

Shrub and herb layers in boreal forests may be virtually non-existent when there is a dense overstory canopy of conifers (Rowe 1955, DeGranpré et al. 1993). In contrast, these layers may be very vigourous under older aspen stands in which the leaf area of the understory might even be greater than that of the overstory (Constabel and Lieffers 1996). As a general rule, understory leaf area is inversely proportional to overstory leaf area (Cannell and Grace 1993). If the overstory captures much of the incoming light, little remains to support the understory (Rowe 1955, Constabel and Lieffers 1996). In Alberta mixedwood forests, light transmission to ground level was of 6% of above canopy PAR in three mixedwood types of different age and overstory composition (Constabel and Lieffers 1996). Similarly in Quebec, transmission to ground level below the understory was 2% in an aspen stand, 7% under birch and pine and 4% under a late successional stand of balsam fir and red spruce (Messier et al. 1998).

Light transmission and competition indices have been recorded for several shrub and herbs that are competitors in clearcut conditions (Vose and Swank, 1990; DeLong 1991, Comeau et al. 1993, Ter Mikaelian et al. 1997) or in open fields (Hirose and Werger, 1995; Tournebise and Sinoquet, 1995). Since leaf inclination and leaf area likely change in the understory, new information must be gathered for understory conditions. Annuals show a peak in leaf area in late spring while most perennials maintain their leaf area over the summer (Uemura 1994).

Given that some shrubs and herbs are deciduous and others evergreen (Uemura 1994), and given the differences in the persistence of and position of leaf litter (Hogg and Lieffers 1991), the amount of shading caused by green leaves and litter will vary seasonally.

Measurement of light in Forests

The following six subsections discuss methods used to estimate light penetration to the forest understory. The first three methods measure light directly through use of quantum sensors or chemical techniques. Light transmission refers to the ratio of PAR measured at some point within the stand compared to PAR incident on the canopy, usually measured in an adjacent clearing or on a tower with a near-complete hemisphere of skyview. These measure transmission of direct and diffuse light, as well as beam enrichment. The other three techniques measure light indirectly through an estimation of canopy openness or gap fraction. These are simplified measures of light transmission: openness is a measure of diffuse skylight transmission (Chadzon and Field 1987) and gap fraction measures diffuse skylight or direct-beam transmission (Norman and Campbell 1989). Both terms ignore the effects of beam enrichment.

1) Light meter measurements

a)Continuous seasonal measurements

Continuous recording of light transmission to a particular microsite, both diurnally and seasonally, using quantum sensors and data loggers is clearly the best method of characterizing the light environment of that microsite over a particular time period. It also provides information on the temporal variation in light. These continuous recordings are often used as the reference light transmittance for comparison with other methods of light estimation (Rich et al. 1993; Easter and Spies 1994; Gendron et al. 1998). Most quantum sensors record light between 400 and 700 nm (Pearcy 1989). For most purposes this is considered to approximate the range of photosynthetically active radiation (Larcher 1981). While other sensors measure energy flux density (irradiance); Pearcy (1989) suggests that PAR sensors better describe the light necessary for plant growth. Commercially available quantum sensors can be used, but the number of microsites that can be measured is usually limited by the cost of sensors. An alternative is to make low-cost sensors using gallium arsenide phosphide (GaAsP) photodiodes (Pearcy 1989, Pontailler 1990, Rich et al. 1993, Easter and Spies 1994; Gendron et al. 1998). These light-weight sensors can even be mounted

on individual leaves (Gutschick et al. 1985). The number of randomly-positioned sensors required for canopy-level estimation depends on the precision required. Reifsnyder et al. (1971) found coefficients of variation (cv) of 121% for pine and 225% for hardwoods values for each sensor averaged over a 5 minute period. If averaged over the entire day, however, the cv dropped to 43% and 13.5%, respectively, indicating that fewer sensors are need to characterize light over days or seasons.

b)Single-time measurements of light

Measurements can be taken with two quantum sensors, one recording light above the canopy and a second below the canopy. The sensor above the stand is connected to a datalogger while the sensor in the understory is connected to a hand-held radiometer/datalogger. This is a simple and inexpensive method for determining %PAR

-Measurements on sunny days

Measurements taken near midday in full sun have been widely used for characterizing light (Carter and Klinka 1992, Comeau et al. 1993, Smith and Riitters 1994, Lieffers and Stadt 1994, Wünsche et al. 1995) but the technique is not well-suited for estimating light at a particular microsite because of the temporal variation in light due to sunflecks or canopy gaps. The average of two readings, one before and one after solar noon is a better indicator of the growing season light transmission to a particular microsite (measured by sensors) than one instantaneous measurement taken at noon (R^2=0.84 for two measurements compared to R^2=0.67 for only one, Gendron et al. 1998).

At a stand level, estimates of light transmission can be determined by averaging instantaneous measurements from a large number of sampling points distributed within the stand (Lieffers and Stadt 1994). Using a hand-held radiometer, Pierce and Running (1988) noted that 30 samples, each the average of 20 measurements, with an 80 sensors radiometer (Decagon Devices, Pullman, WA) taken in a circular sweep, would have 8 to 15% error in the estimation of stand leaf area using Beer's law.

-Measurements on overcast days

Instantaneous measurements of transmittance on overcast days using single sensors show stronger correlation with growing season transmittance than mid-day or entire-day measurements on sunny days (Messier and Puttonen 1995, Parent and Messier 1996, Gendron

et al. 1998). Reifsnyder et al (1971), also noted that on overcast days fewer sensors are needed to characterize light with the same level of precision as on sunny days. In theory, at high latitudes with their lower solar angles, the probability of penetration of the canopy by direct beam light may be lower than the average penetration of diffuse light. In practice, however, the daily percentage of above-canopy light that is transmitted by a canopy is similar on clear and overcast days (Parent and Messier 1996, Messier and Puttonen 1995). The percentage of light transmitted to the understory is stable over the day under overcast skies (Messier and Puttonen 1995). Consequently, the average light transmission at a given point during the growing season (measured using seasonal readings of a quantum sensor) can be estimated from a single instantaneous light measurement taken during overcast sky conditions. In contrast to the hemispherical canopy photographs and LAI-2000 methods (see below), light measurements on overcast days using quantum sensors record the total light in the understory, i.e. diffuse light that comes unimpeded from the sky as well as (light reflected and transmitted by the vegetation. Also, as long as the entire sky is covered uniformly by clouds, light measurements can be taken any time during the day. However, owing to the asymmetry of direct-beam penetration into a gap or around opaque crowns, a diffuse light measurement may under- or overestimate seasonal light transmission (Stadt et al. 1997, Messier and Parent 1997, Gendron et al. 1998) in these situations.

2) Photosensitive paper (ozalid paper)

Light-sensitive diazonium salts on ozalid paper are bleached on exposure to light. When developed with ammonia vapor, the bleached portions of the paper stay white while the rest turns color (Francis 1970). The number of layers of paper bleached is proportional to the light energy received (Friend 1961). Normally, the ozalid paper is left in the understory at particular microsites for a complete day to estimate the integrated daily total radiation value (Kanemasu et al. 1971, Emmingham and Waring 1973, Cole and Newton 1986). Ozalid paper installed in the understory is compared to similar paper installed in an adjacent open area. The technique does not provide a direct measure of PAR but results are expressed as a percentage of light transmission. The advantage of this technique over others is that large numbers of microsites can be sampled by stacks of ozalid paper in petri dishes, thus providing information on both the microsite and stand level. Although relationships between photochemical measurements and measured light are good (R^2=0.99, Friend 1961), the

sensitivity of ozalid paper peaks in the blue and ultra-violet range of the spectrum which is not directly related to the spectral bands used in photosynthesis (Pearcy 1989). Ozalid paper can be used in clear and overcast conditions. Use of neutral density filters increases the period of integration and the accuracy of readings, and decreases the variation among samples (Francis 1970).

Price et al. (1995) used Sunprint photosensitive paper for measuring light interception for selected branches in grape canopies. Similar to the ozalid paper, the Sunprint paper becomes blue under exposure to light. The number of blue pixels, analysed using an image analysis system, is related to light intensity. It is therefore possible to obtain a spatial distribution of light intensity for a short period of time (approximately 5 min). Light estimates from the Sunprint paper and a PAR quantum sensor are highly correlated (R^2=0.93), but the spectral response of the Sunprint paper is unknown. The method allows for measurement of spatial variation of light on small surfaces and papers can be easily shaped to the measured leaves or shoots. Chemical processing, image scanning and analysis are time-consuming.

3) Photochemical methods

Photochemical methods (Marquis and Yelenosky 1962, Wolfenden et al. 1982, Kurachi and Hagihara 1994) typically use a jar of chemical solution that changes colour or solubility on exposure to light, and have been used to estimate PAR in forest canopies under both clear and overcast conditions. These changes are quantified with a spectrophotometer or analytical balance and then related to the quantity of light received during a given period. Correlation coefficients between photochemical light estimates and measured light are strong (R^2 = 0.99, Marquis and Yelenosky 1962), but solutions are also influenced by ultra-violet radiation. As with ozalid papers, sensitivity of the solution does not exactly correspond to the region of the spectrum used in photosynthesis (Pearcy 1989). Photochemical methods, are an inexpensive alternative to estimate light simultaneously at several microsites. However, Wolfenden et al (1982) and Kurachi and Hagihara (1994) have reported some potential problems when using potassium ferrioxalate and anthracene-ethyl solutions. Time spent for the preparation of the solution and the processing with the spectrophotometer add to the costs of these techniques.

4) Hemispherical canopy photographs

Photographs of canopies taken with a 180° field of view lens (Evans and Coombe 1959) are scanned and analyzed with image analysis software to calculate below canopy percent light transmission, sunfleck distribution, R:FR ratio, percentage of canopy openness, and leaf area index (Chazdon and Field 1987, Chen et al. 1991, Rich et al. 1993, Easter and Spies 1994, Wünsche et al.1995, Gendron et al. 1998). The photographs provide a permanent record of overstory canopy geometry relative to an understory position. Analysis of hemispherical canopy photographs allows users to track the movement of the sun over the day and the entire growing season, thereby providing detailed estimation of PAR penetration. Algorithms for analysing canopy photographs, such as the gap light index (GLI) (Canham 1988), give only the percentage of light transmission to the understory, which has been shown to be strongly correlated with measured growing season light transmission ($R^{2=}$0.95, Gendron et al. 1998). Most software used for analysis of hemispherical photographs underestimate background diffuse light found in the understory (Chazdon and Field 1987). Since these programs calculate only light that comes unimpeded from the sky, penumbral light and light scattering are not considered in the calculation of understory light. Some automated analysis programs can be calibrated by long-term sensor measurements to give more accurate prediction of transmitted light (Rich et al. 1993, Whitmore et al. 1993, Easter and Spies 1994). Also, it is difficult to apply this technique in stands with tall shrubs. Despite use of computers and image analysis software, data processing is time-consuming. Careful light exposure is important for successful photographs (Chen et al. 1991). Taking photographs under overcast sky conditions or early in the morning and late in the after noon increases the contrast between the leaves and the sky and facilitates the determining of light threshholds (Chen et al. 1991).

5) Diffuse light transmission using the LAI-2000 Plant Canopy Analyzer

The LAI-2000 Plant Canopy Analyzer is designed to estimate leaf area index, but can also provide an estimate of diffuse light transmission (Gower and Norman 1991, LI-COR 1992) to a particular microsite. It has a 150° field-of-view lens positioned above five concentric light-detecting silicon rings that receive radiation from five different zenith angles (LI-COR 1992). A filter rejects radiation above 490 nm, so the contribution of radiation scattered and transmitted by foliage is minimized. The LAI-2000 can be used on clear sky conditions with view restrictors that block direct beam light. Under completely overcast sky conditions, light estimates calculated with the LAI-2000 and the hemispherical canopy photographs are

strongly correlated (R^2=0.97, (Thormann 1997). LAI-2000 measurements on days with variable sky conditions are also correlated (R^2>0.91) with growing season light transmission (Gendron et al. 1998). Even though the LAI-2000 records only light below 490 nm, these studies demonstrate that diffuse transmission is directly related to PAR in a forest understory. Hanan and Bégué (1995) have also used the LAI-2000 to develop a model for estimating direct light transmission from diffuse non-interceptance. The model effectively simulated the daily variations in light transmission. In the field, the LAI-2000 is easily manipulated. As with hemispherical canopy photographs, beam enrichment is not detected by the LAI-2000 which may result in the underestimation of PAR, especially under shade-tolerant species. One difficulty with the LAI 2000 is obtaining a suitable outside canopy measurement. Users need stable light conditions during the period of measurement or a second LAI 2000 to log conditions outside the canopy while taking readings under the canopy (Welles 1990).

6) Visual estimators of canopy density

The principle of the spherical densiometer (Lemmon, 1956) and the horizontoscope (Schütz and Brang 1995, Thormann 1997) is similar to the hemispherical canopy photograph method. For both devices the image of the canopy above a forest position is projected on a spherical mirror. The spherical mirror of the densiometer is divided into 24 squares, while the horizontoscope has a hyperbolic dome mounted on the top of a circular surface. Each is hand-held and the user visually assesses the amount of the sky not covered with the silhouette of vegetation. The spherical densiometer can be used to estimate the gap fraction while the horizontoscope can also be used to estimate the duration of direct light and percentage of diffuse light transmission received at a particular microsite. Horizontoscope estimates are correlated (R^2>0.86, Schütz and Brang 1995, Thormann 1997) with those of hemispherical canopy photographs. However, the horizontoscope is less accurate under a canopy with many small gaps (Thormann 1997). The horizontoscope is easy to use in the field and light measurements can be recorded on both clear and overcast sky conditions. The moose horn (Robinson, 1947) is another hand-held instrument where the user visually estimates canopy cover in a narrow field of view directly above the user (Bunnell and Vales 1990). All of these instruments have different angle of view of the sky and this results in different estimates of crown completeness (Bunnell and Vales 1990). Since there is no correction for the length of path of view through the canopy at the various angles, the moosehorn (Robinson, 1947) with

its narrow angle of view has a lower estimate of crown completeness than the spherical densiometer with a wider angle (Bunnell and Vales 1990).

These techniques have been used to estimate the light regime of specific points in the understory but since the path of the sun at high latitudes is low in the sky, they are not particularly well-suited for spatially explicit light measurements. Comeau et al. (unpub), however reported a good relationship between spherical densiometer measurements and growing season %PAR (R^2=0.92). With all of these techniques there is variation in estimates among observers and a training program would be necessary to standardize readings (Vales and Bunnell 1988b). A tripod to steady and level the instrument is also recommended.

Models for prediction of light in stands.

Approaches to modeling light beneath forest canopies attempt to link measurements of canopy density and structure to a light transmission probability. The simplest and most widely used approach in agricultural and forestry applications is the Beer-Lambert Law. Its original form is

$$I/I_o = e^{-a\,b\,c} \qquad (1)$$

where I is the light measure at the detector, I_o is the light incident on the absorbing region (I/I_o is the fractional transmission), a is the absorptivity of the objects in the region (dimensionless), b is the path length of the beam through the absorbing region (e.g. in m), and c is a measure of the 'concentration' of the objects (for trees this could be leaf or wood area density, (*LAD*, *WAD*, in $m^2\ m^{-3}$)). The product abc is the absorbance for the region (Swinehart 1962). In ecological applications, some of these absorption parameters are often combined. Key assumptions of the Beer-Lambert Law are that the objects in the absorbing region are randomly distributed in vertical and horizontal space, that these objects reflect and transmit no light, and that the light rays are parallel (Fig. 3a, b). Given the same assumptions, Oker-Blom (1986) demonstrated that the Beer-Lambert Law can be derived from a Poisson process.

The Beer-Lambert Law is applied at various scales depending on the information available. The simplest models treat the entire canopy as the light-absorbing region (Fig. 3a) with an extinction coefficient, k, derived from a calibration of light vs. leaf area index (LAI, m^2m^{-2}), i.e.

$$I/I_o = e^{-k \cdot LAI} \qquad (2)$$

Although it is not apparent, Eqn. 2 embeds the light path length (b). The extinction coefficient (k) is the absorptivity (a) corrected for its projection on a horizontal plane (*i.e.* $k=a/\cos\theta_z$). LAI should be considered the average leaf area per unit gound area along a narrow path through the canopy from the light source. In a homogeneous canopy, LAI is the 'concentration' or leaf area density multiplied by the canopy height (*i.e.* $LAI=LAD \cdot h=c \cdot h$). Canopy height is a function of the light path length (b) and the cosine of its source zenith angle (θ_z), *i.e.* $h=b \cdot \cos\theta_z$. Eqn. 2 is thus consistent with Eqn. 1. This application of the Beer-Lambert Law was introduced by Monsi and Saeki (1953) and has been widely used. In forestry, its most frequent application is to estimate LAI, rather than predict light (Pierce and Running 1988, Dufrêne and Bréda 1995), but the inverse can also be effective. Using an independent estimate of LAI, Pierce and Running (1988), for example, found that Eqn. 2 accurately predicted light transmission in seven conifer stands at two solar angles ($r^2 \geq 0.94$).

Because the equation is relatively simple, an extinction coefficient is required for each stand type. Jarvis and Leverenz (1983) report a range of values of k from 0.28 to 0.65, determined empirically by inversion of Eqn. 2 for pure stands of various species at a given solar angle. However, the extinction coefficient is known to be affected by the angle of incident light and the leaf angle distribution of the foliage (Campbell 1986, Lang 1987; Black et al. 1991, Eqn. 5 below) making it difficult to generalize k for other solar angles and species mixtures. LAI must also be determined, either directly, which is time consuming, or by estimation from relationships between leaf area and sapwood area, which must be established first (Waring and Schlesinger 1985). Most forests are mixtures of species and therefore k and LAI should be determined for each species and combined additively in the model (Eqn. 3) (Cannell and Grace 1993).

$$I/I_o = e^{-\sum_{species} k_{species} \cdot LAI_{species}} \quad (3)$$

Further, equations 2 and 3 are strictly valid only if the effects of boles, branches and beam enrichment are ignored, the leaves are randomly positioned in space, and either the leaves are horizontal (i.e. not inclined) or the light originates from one direction (Oker-Blom 1986). Bole and branch wood plays a significant role in light attenuation (Cermák 1989, Chen 1996), but can be accounted for by basing the extinction coefficient on plant area index (PAI = *LAI* + wood area index, WAI) or adding WAI as another term in the model (cf. Eqn 3). WAI can be measured directly (Sampson and Smith 1993) or PAI estimated by light-interception techniques (Dufrêne and Bréda 1995), although for light predictions the latter results is a somewhat circular process. To account for non-random leaf distribution and leaf inclination requires more effort (see below). The parallel light assumption can be met instead by limiting predictions to clear days when the sun acts as an approximate point source of most of the incident light, or by treating the sun and sky as many small sources of light and integrating transmission along numerous paths.

Sampson and Smith (1993) suggest a model that reflects the change in the extinction coefficient, k with the solar zenith angle (θ_z, Fig. 3b):

$$I/I_o = e^{-G/\cos\theta_z \cdot LAI} \quad (4)$$

where

$$G = a = k\cos\theta_z \quad (5)$$

This formulation extends direct sunlight transmission predictions to all solar angles for predictions at any time of day or season. However, these authors found that G was not independent of *LAI* in 19 lodgepole pine stands, and thus Eqn. 4 predicted light transmission poorly.

A further refinement is to define the absorptivity, *a*, as a separately measurable foliage projection parameter, conventionally symbolized as *G* (Nilson 1971). *G* and *k* are interconvertible using Eqn. 5, and recent studies use either (Campbell and Norman 1989). If the foliage area is inclined as if it were distributed across the surface of a geometric object, such as a sphere or ellipsoid, and the shadow of this object is projected onto a surface perpendicular to the direction of the light source, *G* is the ratio of the shadow area to the upper surface area of the distribution (Campbell 1986, Oker-Blom 1986). A random azimuth orientation is usually assumed, so that only the inclination from horizontal needs to be considered. Values of *G* for known distributions are given by Nilson (1971), Campbell (1986) and Oker-Blom (1986), and usually vary with the zenith angle of the light source. When *G* is ignored, a spherical distribution is implicitly applied, which has a constant *G* value of 0.5 for all source directions. The highly flexible beta distribution (Goel and Strebel 1984) has also been used to model forest foliage inclination (Wang and Jarvis 1990), but requires numerical techniques to approximate *G*. Of course leaf angle is nearly impossible to measure directly on trees, but Norman and Campbell (1989) have developed an iterative inversion process which can parameterize *k* and *LAI* (or *G* and *LAD*, with appropriate modifications) given a number of measurements of direct sunlight transmission taken at different solar angles.

To extend light predictions to cloudy days or over long periods, the Beer-Lambert Law can be applied to the probability of transmitting a single beam of diffuse light through the canopy from each region of the sky (Eqn. 6, Fig. 3c, e):

$$i = i_o(\theta_z, \psi)\cdot\cos\theta_z\cdot e^{-G(\theta_z)\cdot b\cdot LAD} \qquad (6)$$

where *i* is the light reaching a horizontal plane at the measurement point, i_o is the light originating from the sky at a given zenith (θ_z)and azimuth (ψ), the cosine of the zenith corrects i_o to light striking a horizontal surface (Lambert's Law), *G* again is a function of the leaf inclination distribution and the zenith (cf. Oker-Blom 1986), and *b* and *LAD* are as defined above. Eqn. 6 is integrated numerically over the upper hemisphere to calculate diffuse irradiance. Complex functions of the distribution of diffuse sky brightness (i_o) with zenith and

azimuth are available (Oker-Blom 1986), but the degree of cloudiness makes the actual distribution uncertain, so it is often assumed that all areas of sky are equally bright (Canham et al. 1994, Ter Mikaelian et al. 1997). Several studies (Canham et al. 1994, Ter Mikaelian et al. 1997) have developed a "seasonal sky" which has sectors whose brightness is the product of the time the solar track passes through the sector, the direct beam light irradiance at that sector's zenith, and the likelihood of that sector not being obscured by cloud (Fig. 3d). Diffuse light could be incorporated into the i_o values for these sectors, so that integration of Eqn. 6 over these sectors would give the total seasonal light.

The effects of non-random distribution of foliage horizontally and vertically within the canopy in simulation studies was found to be the next most important factor after *LAI* in predicting light transmission (Sampson and Smith 1993, Larsen and Kershaw 1996). An attempt to include between-crown gaps in a Beer-Lambert Law model was not fruitful (Sampson and Smith 1993). Positive and negative binomial distributions or Markov models (Nilson 1971, Sinclair and Knoerr 1982, Oker-Blom 1986) have been suggested as alternatives to the Beer-Lambert Law for nonrandom foliage distributions, but estimating these models' parameters is not straightforward. Pukkala et al. (1993) and Canham et al. (1994) took another approach, and used spatially-mapped tree crowns, modeled as cylinders or ellipsoids, as multiple light-absorbing regions (Fig. 3c). This accounts for gaps and the horizontal aggregation of foliage into crowns. In these models, light transmission depends on the sum of the path lengths within the crowns through which light beams pass on their way from the sky to the measurement point. Pukkala's pure Scots pine model used allometrically-determined projected leaf area density (*pLAD* = the projected leaf area per tree divided by crown volume), equivalent to *G*×*LAD*, to convert within crown length (*b*) into absorption (Eqn. 7):

$$i = i_o(\theta_z, \psi) \cdot \cos\theta_z \cdot e^{-\sum_{species} \sum_{tree} pLAD_{species,tree} \cdot b_{species,tree}} \qquad (7)$$

(Pukkala et al. (1994) multiplied transmission values rather than added absorbances; these are equivalent). The absolute path length variant of Canham's mixedwood model also combines foliage projection and *LAD* into species-specific extinction coefficients equivalent to projected

leaf area density (*pLAD*), except these were determined by maximum likelihood regression of the sum of the path lengths through crowns of each species on canopy openness as determined by hemispherical photography. The predictions of Pukkala's model were correlated with measured light transmission ($r \geq 0.69$) and showed a similar spatial distribution; seedling growth correlated with predicted light as well. For Canham's model, predictive accuracy is harder to evaluate. Openness calculated by the model appears to be correlated with the estimate determined from hemispherical photographs, but no independent validation was performed.

Korzukhin and Ter Mikaelian (1995) also developed a spatially-explicit model where individual trees or shrubs are represented by vertical or horizontal planar screens of appropriate shape that are semi-transparent to light. The model estimates the amount of light passing through the screens and between the trees to specific ground positions. It is similar in approach to the "hits" variant of Canham et al.'s (1994) model. For species with long crowns and multiple layers, Ter Mikaelin et al. (1997) refined the model to use multiple horizontal screens, each representing a single uniform layer of leaves with the correct horizontal size and approximate vertical position (Fig. 3d). The issue of within-crown foliage distribution can then be addressed as well, particularly for species with tiered, whorled branch structure. With good estimation of leaf area and extinction coefficients for the screens, estimation error was less than 8% of the measured light.

Several other attempts have been made to model within-crown foliage distribution. Norman and Welles (1983) applied the Beer-Lambert Law to nested subcrown regions of different leaf area density. Individual tree crowns were modeled as nested ellipses, and transmission was calculated as the sum of the subcrown absorbances (projected *LAD*×path length through each subcrown region)

$$i = i_o(\theta_z, \psi) \cdot \cos\theta_z \cdot e^{-\sum_{\text{tree}} \sum_{\text{subcrown}} pLAD_{\text{tree, subcrown}} \cdot h_{\text{tree, subcrown}}} \qquad (8)$$

Norman and Jarvis (1975) took cylindrical single-cohort shoots as the light-absorbing region of their Sitka spruce light transmission model. These were grouped into flat, circular whorls

positioned along a stem. The proportion of the horizontal area occupied by these whorls when projected toward the light source, the probability of hitting a shoot within a whorl at this angle, the transmission through the shoot cylinder, as well as the contribution of reflection and through-leaf transmission were used to calculate light flux through successive canopy layers (see below). Wang and Jarvis (1990) distributed leaves vertically through the live crown and horizontally from the stem according to density functions fit to harvested trees. Transmission through these trees was calculated as with Norman and Welles (1983). Oker-Blom et al. (1991) developed a hierarchical model of light transmission, in which light can be absorbed by individual leaves, shoots, or crowns (Fig. 3e), to determine the relative importance of leaf size, area and inclination, shoot area and distribution, and stem distribution in the stand on model predictions. *LAI* was poorly estimated, confounding the analysis, but this paper laid the groundwork for modeling light transmission at any of these levels. The crown-absorption variant of this model produced estimates of light transmission within 8% transmittance of the measured value for four pure lodgepole pine and one Engelmann spruce stand (Oker-Blom 1991).

The contribution of beam enrichment, the reflection and through-leaf transmission of direct sunlight and diffuse light, is the most difficult aspect to model. Canham et al. (1994) calculated direct-beam enrichment as the difference between diffuse light predicted by their model and measured light at times when the sun was shining but not striking the measurement sensor. From this estimate, they suggested that beam enrichment could account for 14-41% of the understory irradiance. Norman and Jarvis (1975) modelled beam enrichment by measuring leaf reflection and through-leaf transmission values, converting these, and the leaf distribution information (see above) to vertical upward and downward transmission/reflection coefficients for thin horizontal layers of canopy. To model the entire light environment, an iterative approach was taken. First, upward and downward reflection was evaluated layer by layer from the ground, starting with the soil reflectivity, to the top of the canopy. This yielded a starting ratio of diffuse light tending upward to diffuse light tending downward at each layer. Transmission, reflection, and absorption of diffuse skylight was then evaluated layer by layer from above the canopy to the ground. The process was iterated several more times, but with both direct-sunlight and diffuse light fluxes considered, until the upward- and downward-

tending light estimates at each layer were stable (Fig. 3f). By accounting for leaf transmission and reflection, the direct and diffuse light scattered by each layer could contribute to the layer's estimate of total diffuse flux. The predictive accuracy of this model appears to be good. The stand-average transmission at 4 heights was predicted closely by the model (Fig. 11 of Norman and Javis 1975). Using a modeling approach that combined the Norman and Jarvis (1975) radiative transfer approach with a light ray tracing model similar to Pukkala et al. (1993) and Canham et al. (1994), Wang and Jarvis (1990) found the difference between predicted and measured transmission for Sitka spruce and radiata pine stands was less than 10%. However, in addition to the required information on the leaf area density, spatial distribution, and inclination angle distribution, information on transmission and reflectivity of leaves and stems must also be obtained for each species involved.

Application of these models to the estimation of stand development has been hindered by lack of specific calibration data for the individual stands in question. The methodologies, listed above for measurement of light within forests are useful for describing individual stands, but have not been used for prediction of light in a large number of stands, such as in a forest management unit. High costs for estimation of such factors as foliage inclination, clumping and stem mapping, make some of the above models impractical for application to a large number of stands. Furthermore, the effect of the understory vegetation is not usually taken into consideration, and the spatial (point-by-point) accuracy of many of the models has not been evaluated. As a result, consideration of light transmission and prediction of understory development are usually not incorporated in stand level planning. A goal for further modeling would be to use the data collected in a normal timber cruise or permanent sample plot e.g., a stem map with species, diameter, height, height to live crown, crown width, and understory species cover as the model input.

Management of light in Forests

While managers have no control of above-canopy light, they can control the light levels in the understory by controlling the amount, position and type of vegetation that absorbs the incoming light. The benefits from controlling light include: 1)promoting establishment and early development of tree seedlings, thereby establishing the next generation of trees,

2)managing the growth of lower strata of trees in uneven aged and mixed species management systems, 3)controlling the growth of understory shrub/herb layers either to suppress their growth as competitors or promote their growth for wildlife habitat or biodiversity reasons. With an understanding of the density and position of shading leaf area and the way that stands develop naturally, managers can identify or create windows of opportunity for developing appropriate light regimes for these goals suggested by the following examples.

Manipulation of Overstory Density

In a relatively stable forest system, the biomass of the understory is inversely correlated with the density of the overstory (Zavitkovski 1976, Cannell and Grace 1993, Brown and Parker 1994, Lieffers and Stadt 1994, Ricard and Messier 1996). A long-term strategy for controlling shrub and herb competition during the regeneration phase is to develop dense overstory canopies at the end of the rotation. Persistent competitors such as *Rubus idaeus* (Ricard and Messier 1996) or *Calamagrostis canadensis* (Lieffers and Stadt 1994) can be eliminated from the understory if light is below 10% of above-canopy light. In the subsequent regeneration phase, there may be a delay in the redevelopment of these plants as they must recruit from seed rather than from a bud bank (Tappeiner et al. 1991). Knowledge of the speed of recruitment and growth of the shrub/herb layer is critical to estimating the period of increased light at the ground level following overstory thinning. This has rarely been studied (Hannerz and Hånell 1993).

Reducing overstory density in shelterwood and selection systems or commercial thinning (e.g. Oliver and Dolph 1992; Johansson 1987) temporarily destabilizes the balance between overstory and understory canopies, allowing increased light transmission to the understory and ground surface (Fig. 4). Managers might match the light transmission to the understory with the light requirements for growth of target species. For white spruce seedlings, the light required for maximum photosynthesis of an individual twig is between 40% and 60% of full sunlight (Man and Lieffers 1997), while volume growth is linearly related to light transmission (Comeau et al. 1993, Chen et al. 1996, Klinka et al. 1992). In the regeneration phase, managers may choose to retain a relatively dense overstory and sacrifice some of the growth rates of saplings for several reasons. 1) In dry sites, daytime radiation loading may overheat regeneration if too much overstory is removed (Holbo et al. 1985). 2) In colder areas,

nighttime radiation losses and night frosts are reduced in partial-cut areas compared to clearcuts (Groot and Carlson 1996). 3)When there are aggressive shade intolerant shrubs, grasses or herbs a residual overstory can inhibit their growth more than the height growth of shade tolerant tree seedlings (e.g. *Rubus idaeus* (Ricard and Messier 1996), *Epilobium angustifolium, Calamagrostis canadensis* (Lieffers and Stadt 1994) and *Gaultheria shallon* (Messier et al. 1989)). Thus, for tree regeneration, the amount of residual canopy could be balanced to deliver sufficient light to allow establishment of the desired trees but avoid competitors and temperature extremes.

The rate at which tree canopies close after partial removal of the overstory will depend on the proportion of the original stand remaining and on the rate of horizontal expansion of crowns (Smith et al. 1997). Over time, this will gradually result in reduction of light to understory layers (Fig. 4) closing the window of opportunity.

Removal of the overstory in patches and strips results in large openings for light transmission (Berry 1964). The orientation of these opening influences the regeneration environment in the understory. At high latitudes, narrow strips oriented E-W will result in patches of strong light under the crowns of adjacent residual trees and light conditions will be similar to that of small gaps (Canham 1988). Some shelterwood systems orient the cut face E -W to encourage illumination and regeneration under adjacent residual trees (Matthews 1989). Strips oriented N-S will have brief periods of high illumination at noon.

Site preparation of the understory.

Removal of the shrub/herb layer by chemical, or mechanical means also temporarily destabilization of the understory vegetation, making the overstory the only significant barrier to light (Fig. 5b). Blading out the roots and rhizomes of understory plants reduced shading for five years (Lees 1970). Provided tree recruitment is early, this period may be sufficient to establish tree seedlings.

Concluding Remarks

We have attempted to outline part of the massive body of literature on light in forests, including the different approaches for measuring, modelling and manipulating light

availability and quality in forest stands. Implications for regenerating tree species have been discussed. We now identify a number of areas for further study, listed in the same order of topics as in the review: 1) The seasonality of understory light availability in relation to the photosynthetic activity of understory plants needs more work. How much do these plants, particularly regenerating evergreens, improve their carbon gain at the times when the overstory is leafless? 2) Does the importance of gaps in forest dynamics decline with latitude, owing to the spatial offset of the position receiving additional light relative to the region with increased soil moisture and nutrients? 3) Thresholds for sunflecks should be related to the light demands of the understory species. Since sunflecks may not be as significant in well-lit understories, a strategy for sunfleck measurement needs to be developed that recognizes the significance of background light levels. 4) More ecological work should be done to determine effects of spectral characteristics other than R:FR on understory plant performance. 5) The distribution of leaf area and leaf area inclination in the understory canopy and its effects on the light profile for growing trees need further study. 6) Further modelling of beam enrichment in forests is needed to improve the spatial accuracy of indirect light measurements. 7) Simulation models of light transmission should be modified so that standard forest inventory data can be used as input rather than the extensive and specific data required by present models. This would allow light availability to be used as a predictive management tool. 8) Response of forest regeneration following silvicultural treatments such as thinning, partial-cutting, or site preparation should be linked to estimates of light at ground level.

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Table 1 Sunfleck threshold, duration of measurement period and percentage of daily light on sunny days contributed by sunflecks for a range of northern forests.

Authors	**Stand type and Location**	**Sunfleck Threshold (μmol m^{-2} s^{-1})**	**Duration of Measurement**	**Sunfleck % Contribution to total PAR**
Chen and Klinka 1997	Douglas fir, Pacific Northwest	50	< 18days	32
Messier and Puttonen 1995	Mature Scots pine, Finland	90	4-7 days	90
Messier and Puttonen 1995	Open 7-year-old Scots pine, Finland	350	4-7 days	65
Lei and Lechowicz 1990	Eastern deciduous	100	Samples over 16 days	53
Messier et al. 1998	Boreal forests of eastern Canada: - aspen - white birch - 3 deciduous-coniferous stands - fir-white spruce - black spruce - jack pine	100	One full sunny day	 59 75 60-70 79 69 86
Messier et al. 1998	Mixed boreal forests of Quebéc: - aspen - white birch - mixed deciduous-coniferous -fir-white spruce -black spruce - jack pine	250	One full sunny day	 28 53 51-57 56 32 49

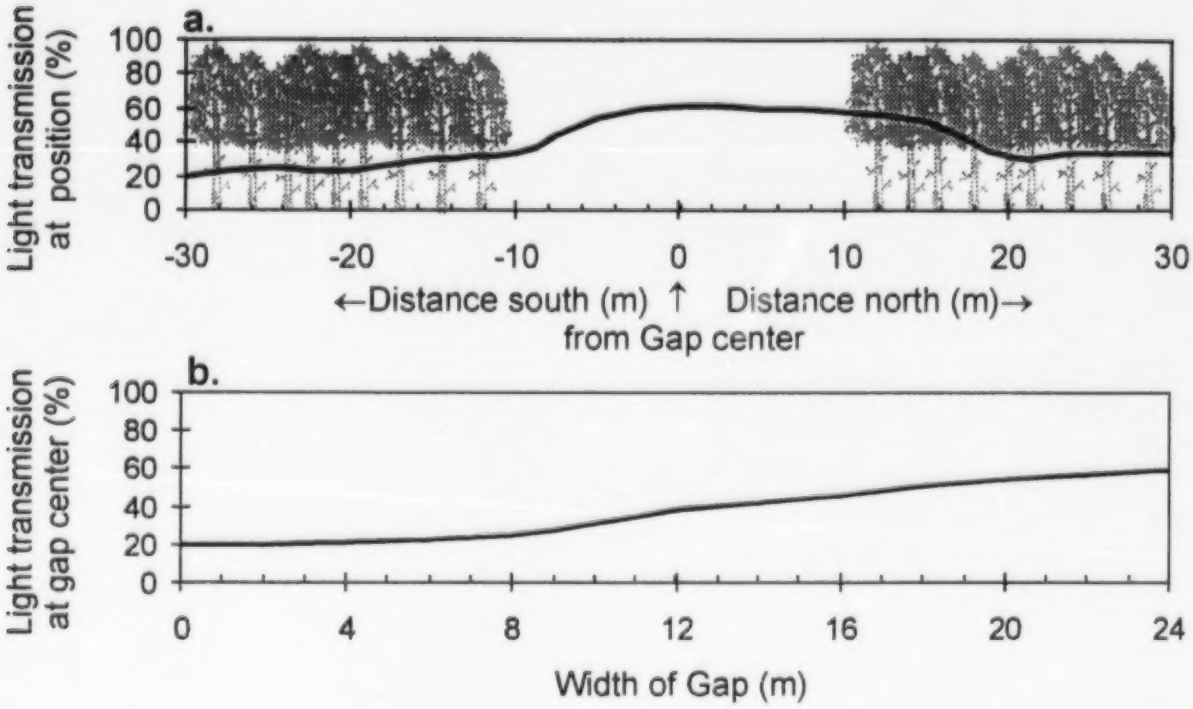

Fig. 1. a) The effect of gap position on seasonally-integrated light transmission. This gap is 24 m wide in a homogeneous birch stand 10 m in height (Comeau et al. 1998). b) The effect of gap size on seasonally-integrated light transmission at gap center (Comeau et al. 1998).

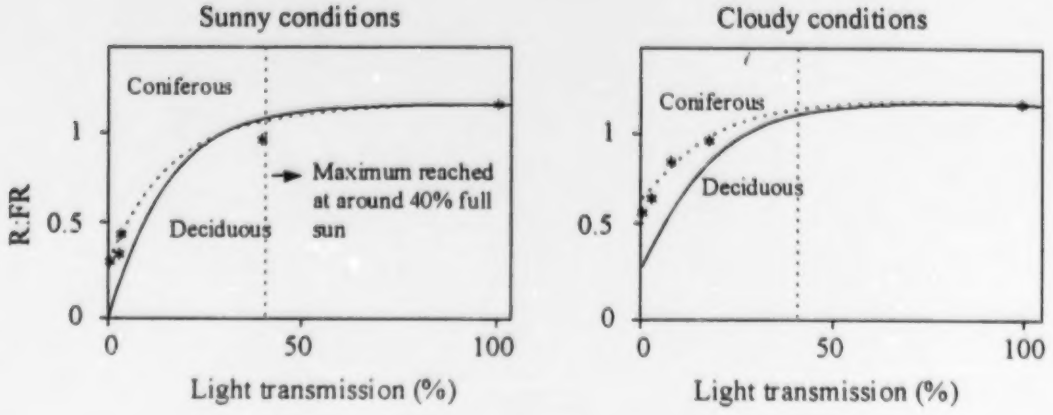

Fig. 2 Idealized relationships between R:FR and PPFD under coniferous vs. deciduous dominated stands under completely sunny or cloudy conditions. The lines drawn for coniferous stands under sunny and cloudy conditions are based on data from Messier & Puttonen (1995) under pure Scots pine stands in Finland and on data points (*) from Messier et al. (1989) under pure stands of western hemlock and western red cedar. These relationships were also checked with data from Ross et al. (1986), Ritchie (1997) and Mailly & Kimmins (1997). The line for deciduous stands under sunny conditions is based on continuous data points covering the range from 1 to 100% full sunlight collected under pure stands of broad-leaf maple in Coastal B.C. by Gendron (Unpublished), and data from Messier & Bellefleur (1988), Morgan & Smith (1981), St-Jacques & Bellefleur (1993), Endler (1993) and Lei et al (1998). The line for deciduous stands under cloudy conditions is based on data from Messier & Bellefleur (1988), Morgan & Smith (1981), Endler (1993) and Lei et al. (1998).

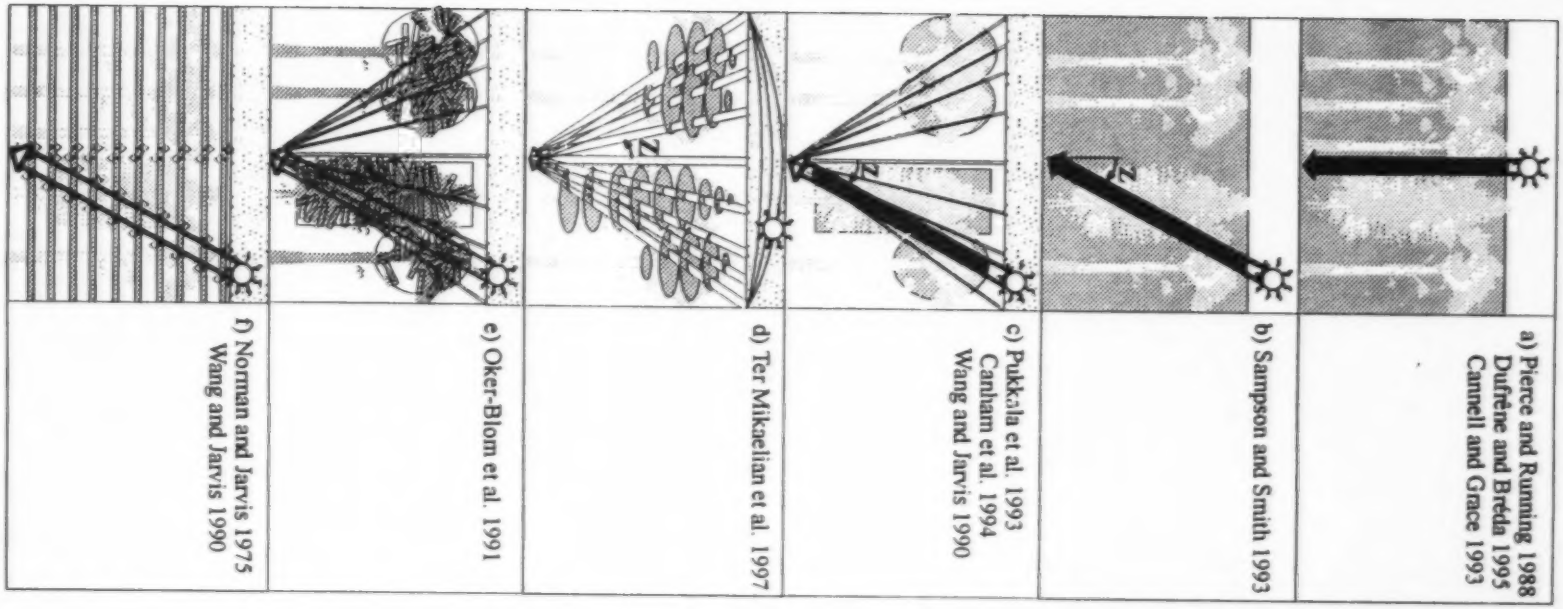
a) Pierce and Running 1988
Dufrêne and Bréda 1995
Cannell and Grace 1993
b) Sampson and Smith 1993
c) Pukkala et al. 1993
Canham et al. 1994
Wang and Jarvis 1990
d) Ter Mikaelian et al. 1997
e) Oker-Blom et al. 1991
f) Norman and Jarvis 1975
Wang and Jarvis 1990

Fig. 3. Pictorial representation of the light transmission models. The actual canopy structure is shown in light gray. The medium-gray area in each frame is the light-absorbing region, which can be canopy (a, b), crown (c, d, e), shoot (e), leaf (e), or layer (f). The sources of light are shown above each canopy: the sun (radiating globe), skylight (stippled bar), or "seasonal sky" (stippled bar with the solar track; see text). Paths taken by light from these sources through the canopy are shown by arrows: the wide arrow represents the path taken by direct sunlight, the narrow arrows are diffuse skylight. Where the "seasonal sky" is the light source, medium arrows are used. Arrows are black where they pass through the models' light-absorbing regions. "Z" is the zenith angle.

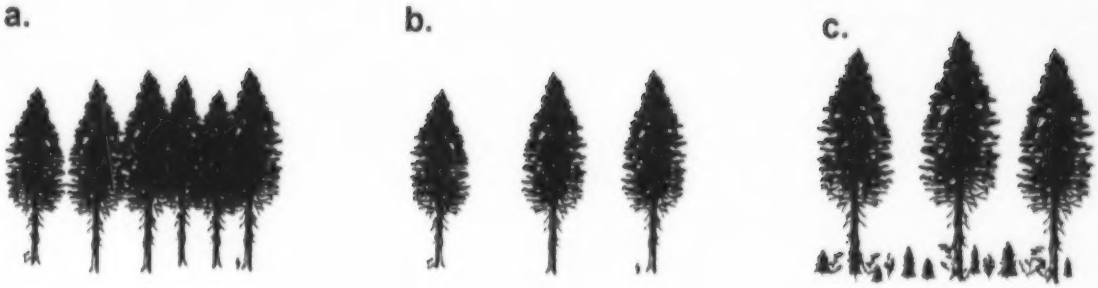

Fig. 4. Understory canopy of an intact dense conifer stand 2a, immediately after thinning 2b and five years later 2c. The dense overstory virtually eliminates the understory. The period after thinning allow increased light to ground level but this period is short-lived as the understory eventually colonizes this space.

Fig. 5. Understory canopy of a mature aspen stand 3a, immediately after strip understory site preparation 3b, and five years later 3c. The porous overstory of the aspen allows a heavy understory to develop. The strip site preparation provides a temporary increase in light to ground level but the understory eventually redevelops.